IDENTIFYING DISRUPTIONS OF POPULATION PROCESSES IN FRAGMENTED LANDSCAPES FOR AN ENDEMIC HABITAT SPECIALIST, THE DUNES SAGEBRUSH LIZARD (*Sceloporus arenicolus*)

A Dissertation

by

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ABSTRACT

Habitat fragmentation and habitat loss are two of the main drivers of biodiversity loss. This anthropogenic reduction of habitat and the corresponding increasing isolation can lead to negative consequences for biodiversity including species loss, changes in community composition, and reduced species diversity at multiple levels of organization. Understanding how a species is distributed across the landscape is especially important in conservation contexts, as variations in habitat quality can drive population persistence. My dissertation focused on *Sceloporus arenicolus* (dunes sagebrush lizard) a habitat specialist endemic to the Mescalero Monahans Sandhills ecosystem threatened by loss and degradation of shinnery oak dunes. Extensive development of well-pad and road networks has led to fragmentation of shinnery oak dunes, negatively impacting *S. arenciolus* populations. I utilized data from three different studies to elucidate responses of *S. arenicolus* populations in highly fragmented areas, understanding how *S. arenicolus* use and move through habitat, and finally estimating occupancy probabilities across part of its Texas range.

To understand how populations of *S. arenicolus* and other dune-dwelling lizards in the community were impacted by landscape fragmentation, we captured lizards on 27 independent trapping grids located in unfragmented (N=18) and fragmented (N=9) sites in southeastern New Mexico from 2009 to 2013. Using a two-way ANOVA, we tested for effects of fragmentation and year on capture rates for each species. Capture rates of *S. arenicolus* decreased to zero in all fragmented sites. Before extirpation, the demographic structure of *S. arenicolus* and *Holbrookia maculata* (common lesser earless lizard), were

severely disrupted at fragmented sites, with proportions of juveniles, adult males or adult females being over or under represented during sample months. To understand patterns in use, settlement, and vacancy at both the microhabitat and landscape scales at two different sites, we trapped *S. arenicolus* at two different trapping sites (~14 ha each). For each site individually, we modeled use, settlement, vacancy, and detection as functions of microhabitat and landscape variables in separate analyses. I showed that microhabitat and landscape context influence use, settlement, and vacancy patterns in complex ways; these patterns were dynamic and no single variable consistently predicted the dynamics among the patterns. Microhabitat variables better predicted the probability of use, while landscape-scale variables better predicted probabilities of settlement and vacancy.

Finally, to gain a baseline understanding of occupancy in parts of the range of *S. arenicolus* in Texas using the range map from the Texas Conservation Plan, 100 16-ha sites were surveyed multiple times (336 surveys total) from May to August 2014–2016. Thirty-three *S. arenicolus* were detected during 17 surveys at nine sites in areas classified as Very High likelihood of occurrence. Occupancy probability for *S. arenicolus* in the Very High likelihood of occurrence areas was 0.32 ± 0.09 (SE), with a detection probability of 0.52 ± 0.12. Local extinction probabilities were low at 0.12 ± 0.18, with the colonization probability fixed at zero. No *S. arenicolus* were detected in the 54% of surveys that occurred outside the currently recognized range.

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CHAPTER I

INTRODUCTION

Habitat fragmentation and habitat loss are two of the main drivers of biodiversity loss (Dirzo and Raven 2003, Bellard et al. 2014). Anthropogenic reduction of naturally occurring vegetation associations and increasing isolation of these areas can lead to negative consequences for biodiversity including species loss, changes in community composition, and reduced species diversity at multiple levels of organization (Andrén 1994, Saunders et al. 1991). One of the major causes of fragmentation is construction of roads. Roads have specific characteristics that may enhance the effects of fragmentation (van der Ree et al. 2011), which other types of fragmentation such as the forest/agriculture matrix may not have (e.g., Driscoll et al. 2012, Michael et al. 2017). As roads are built, they open up the area for development, intensifying the effects of the landscape fragmentation by acting as corridors for invasive species, increasing edge effects, and act as a barrier to movements (Forman and Alexander 1998, Frair et al. 2008, Trombulak and Frissell 2000).

Multiple studies have shown that species with more specific habitat requirements (specialists) respond poorly in fragments, with lower abundances or even local extinction, although habitat specificity is usually not considered explicitly in the models (Sarre et al. 1995, 1996, Barrows and Allen 2007, Lion et al. 2016, Russildi et al., 2016). However, the context of the habitat changes is important, as Attum et al. (2006) showed in a study of desert specialists and generalists. In that case, desert specialists actually did better in degraded areas that were undergoing desertification, consequently increasing their

available habitat and reducing competition by filtering out generalists that utilize more vegetated areas of the desert.

Finally, dispersal ability also is influenced by fragmentation across studies, showing that in general, lizards that are better dispersers through an intervening matrix tend to have larger and less genetically structured (meaning more gene flow) populations (e.g., Díaz et al. 2000, Driscoll 2004, Hoehn et al. 2007, Levy et al. 2010, Munguia-Vega et al., 2013). However even within the studies examining effects of fragmentation on lizards, much work has focused on species that occupy forest-agricultural landscapes, with much less attention given to other forms of habitat fragmentation.

Configuration of distinct habitat patches, matrix, and corridors may be important in mitigating species' responses to habitat fragmentation, but not until a lot of habitat is lost (Fahrig 1997, Andrén 1994). Multiple researchers have found in simulation studies that configuration of remnant fragments can play a part in species persistence in fragmented habitats (Cantrell and Cosner 1991, With and Crist 1995, Hill and Caswell 1999). However, even continuous habitats are not usually homogenous but can be made up of a mosaic of patches of resources (Merriam 1995, Shaver 2005). The configuration of these mosaics of varying quality influences species' distributions through patterns of dispersal of individuals, populations, and species across landscapes over time (González-Megías 2005, Turner and Chapin 2005, Ryberg et al. 2015). Understanding how a species is distributed across the landscape is especially important in conservation contexts, as variations in habitat quality can drive population persistence (Ye et al. 2013a, b).

Like many groups, squamates have experienced population declines as a result of many causes, including habitat loss and degradation (agriculture, natural resource use, and

urban development), pressure from invasive species, and resource harvesting (Gibbons et al. 2000, Böhm et al. 2013, Fitzgerald et al. 2018). Although population declines may be pervasive, they are also hard to detect, because reptile population abundances can vary widely over time from natural causes (Fitzgerald 1994, Mazerolle et al. 2007, Hibbitts et al. 2009). Temporal variation in the abundance or occurrence of reptile populations is notoriously stochastic, and presumed to be associated with fluctuating environmental conditions (e.g., drought), variable resources (Dunham 1981), and many other factors. Determining whether a decline is part of natural population fluctuations or driven by human activities poses a challenge for species conservation (Gibbons et al. 2000).

The Mescalero-Monahans Sandhills ecosystem, located in southeastern New Mexico and adjacent west Texas, overlying the Permian Basin, is comprised of ancient parabolic dunes maintained by wind, moving sand, and partially stabilized by *Quercus havardii* (shinnery oak; Hall and Goble 2008). The system is characterized by a patchy arrangement of open dune blowouts (bowl-shaped depressions formed when sand is blown against the leeward slope with vegetated arms extending around the sides) in a matrix of shinnery oak flats (Fitzgerald and Painter 2009, Ryberg et al. 2015). The Permian Basin is the world's second largest oil field and produces approximately 14% of the United States' crude oil (Ewing et al. 2014). Networks of roads built for oil and gas development results in persistent landscape fragmentation (Smolensky and Fitzgerald 2011, Leavitt and Fitzgerald 2013) and these fragmented areas have more compact soils, shallower slopes, and less shinnery oak, which are strong indicators of degraded dune blowout landforms in this habitat (Hibbitts et al. 2013). The lizard community in this system is composed of species ranging from widespread generalists to an endemic habitat specialist. In highly

fragmented areas, the lizard community becomes disassembled, changing from a predictably structured community to one that is randomly structured following the local extirpation of *Sceloporus arenicolus* (dunes sagebrush lizard) and *Holbrookia maculata* (common lesser earless lizard; Leavitt and Fitzgerald 2013).

Sceloporus arenicolus is a habitat specialist threatened by loss and degradation of shinnery oak dunes, endemic to the Mescalero Monahans Sandhills ecosystem (Fitzgerald et al. 1997, 2011, Laurencio et al. 2007, Laurencio and Fitzgerald 2010). Within this ecosystem, *S. arenicolus* exclusively uses the mosaic of dune blowouts in the shinnery oak matrix (Fitzgerald and Painter 2009). At the local scale, *S. arenicolus* select larger blowouts with steeper slopes, lower substrate compaction, medium sand grain sizes, and less vegetative cover (Fitzgerald et al. 1997, Smolenksy and Fitzgerald 2011, Hibbitts et al. 2013). *Sceloporus arenicolus* are spatially distributed in neighborhoods (*sensu* Addicott 1987, localized groups of interacting individuals within a continuously distributed population; Ryberg et al. 2013) and survivorship and fecundity in neighborhoods were tightly linked to the configuration of dune blowouts in the landscape. Even in areas considered highly likely to contain *S. arenicolus,* they show a patchy distribution, and there are areas in the dune blowout landscape where we expect to find them and do not (Fitzgerald et al., 1997, 2011).

Range-wide occupancy and persistence of the *S. arenicolus* is affected by large-scale and persistent conservation challenges. *Sceloporus arenicolus* exhibits road avoidance behaviors toward even small, rarely traveled roads (Hibbitts et al. 2017), so the network of the road infrastructure appears to disrupt the movement dynamics across the landscape. With the extensive threats to *S. arenicolus* populations and habitat in Texas and

the impetus from its proposed listing under the Endangered Species Act (US Fish and Wildlife Service 2010), the Texas Conservation Plan (TCP; Texas Comptroller of Public Accounts 2012) was put into place in 2012. The TCP is a conservation agreement with assurances that relies on voluntary participation built on a partnership among private landowners, industry, and state and federal agencies. The aim of the TCP is to incentivize participants to avoid habitat conversion for the *S. arenicolus* in Texas, minimizing the perceived risks of federal listing of the *S. arenicolus*.

In Chapter II, I evaluated the effects of landscape fragmentation on capture rates and the demographic structure of multiple lizard species in the Mescalero-Monahans Sandhills ecosystem in New Mexico. Using a two-way ANOVA, I tested for effects of fragmentation and year on capture rates for each species. To test for effects of fragmentation on demographic structure, I used contingency tables with expected frequencies computed from the average demographic structure on unfragmented grids. This chapter provides insights into how landscape fragmentation disrupts the population structure of an ecological specialist species, and how species in ecological communities vary in their response to fragmentation.

In Chapter III, I examined the probabilities of use, settlement, and vacancy of *S. arenicolus* across continuous habitat, including covariates that quantify both microhabitat and landscape-scale variables. This allowed me to examine how *S. arenicolus* populations used habitat and movde through habitat and helped to identify drivers of this use and movement, to better predict the scale at which *S. arenicolus* was utilizing habitat.

Finally, in Chapter IV, I created an occupancy model for the Dunes Sagebrush Lizard to increase our understanding of the pattern of presence and absence of the species,

across its range in Texas. Using multi-season occupancy models, I estimated occupancy (ψ), detection probability (p), colonization probability (γ) and local extinction probability (ε) for the sites in the Very High likelihood of occurrence areas from the Likelihood of Occurrence map used in the TCP (Texas Comptroller of Public Accounts 2012). Additionally, I used the occupancy model results to lend insights into the previously established areas of likelihood of occurrence.

CHAPTER II

EFFECTS OF HABITAT FRAGMENTATION ON POPULATION STRUCTURE OF DUNE-DWELLING LIZARDS[*]

Synopsis

Landscape fragmentation alters biotic and abiotic characteristics of landscapes, variously affecting the size and demographic structure of species' populations. Fragmentation is predicted to negatively impact habitat specialists because of perturbations to their habitat, whereas generalists should be less sensitive to fragmentation. Differences in life history among the lizards in this community should partly explain some of the variation in generalist species responses to fragmentation. During five seasons (2009-2013), we captured eight species of lizards on 27 independent trapping grids located in unfragmented (N=18) and fragmented (N=9) grids in the Mescalero-Monahans Sandhills ecosystem in southeastern New Mexico. Using a two-way ANOVA, we tested for effects of fragmentation and year on capture rates for each species. To test for effects of fragmentation on demographic structure, we used contingency tables with expected frequencies computed from the average demographic structure on unfragmented grids. Capture rates of the endemic habitat specialist *Sceloporus arenicolus* (dunes sagebrush lizard) decreased to zero in fragmented sites. The demographic structure of *S. arenicolus* and *Holbrookia maculata* (common lesser earless lizard), were severely disrupted at

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fragmented sites, with proportions of juveniles, adult males or adult females being over or under represented during sample months. Variable responses of five generalist species could be attributed to life history patterns, habitat affinity, and breeding phenology. This is the first empirical study we are aware of that describes and quantifies the demographic effects of fragmentation on populations of multiple lizard species in a replicated study. Our findings lend important insights into how habitat specialization and differences in life history influence the susceptibility of species to the impacts of fragmentation.

Introduction

Habitat loss and landscape fragmentation are considered primary drivers of biodiversity loss (Brooks et al. 2002, Dirzo and Raven 2003, Bellard et al. 2014). However, studies of vertebrate and invertebrate communities show that individual species respond to landscape fragmentation differently; some species thrive while others decline (Haila 2002, Fahrig 2003). Fragmentation can cause population declines in vulnerable species by disrupting processes such as dispersal, gene flow, recruitment, and survival (Hokit and Branch 2003, Henle et al. 2004, Mitrovich et al. 2009). However, broad variations in species' specific responses to fragmentation have made it difficult to identify general trends that predict how a species may respond to fragmentation (Betts et al. 2014).

In an attempt to identify general trends in species responses to fragmentation, Andrén et al. (1997) and Henle et al. (2004) predicted that habitat specialists would be more sensitive to fragmentation because they are dependent upon relatively restricted habitat types. Alternatively, habitat generalists are likely to be less sensitive to fragmentation and may even thrive in disturbed and changing landscapes because of their broader habitat tolerances, benefitting from the increased landscape heterogeneity, more

edge habitat, and competitive relaxation associated with fragmentation (Henle et al. 2004, Devictor et al. 2008). This prediction has been supported in taxonomic groups, such as birds and insects (Warren et al. 2001, Kotze and O'Hara 2003, Goulson et al. 2005, Devictor et al. 2008) and has been identified as a good predictor for some reptile species (Mac Nally and Brown 2001, Hibbitts et al. 2009). However, this dichotomy does not describe all the variation seen in the responses of lizards to fragmentation, and generalist species can also show declines in fragmented areas (e.g., Driscoll 2004, Attum et al. 2006). As such, the contrast between habitat specialists and generalists could be a useful framework, if integrated with other characteristics of the species, in predicting the likelihood of lizard species being sensitive to fragmentation.

Theory predicts that a typical population is characterized by a relatively stable age structure and sex ratio, with natural seasonal fluctuation (Fitzgerald 1994, Gotelli 1995, Caswell 2001, Le Galliard et al. 2005). In species that experience seasonal birth pulses, including many lizard species in temperate areas, the age structure corresponds to a predictable yearly phenology, with relatively high proportions of adults and young-of-year at the beginning of the breeding season, a peak in the proportion of adults during the middle of the breeding season as juveniles mature, and a peak in proportions of juveniles near the end of the breeding season as hatchlings emerge (Bustard 1969, Fitzgerald et al. 1999). Over many years, the age structure is expected to be stable, despite the seasonal changes.

However, age or stage structure varies among species and is strongly associated with their life history strategies. Populations of species with early maturation, short life span, and high fecundity have relatively high proportions of juveniles after reproduction

has occurred, which reverts to very low proportions of juveniles the next spring (Alcala and Brown 1967, Tinkle 1973, Dunham and Miles 1985, Barbault and Mou 1988). Alternatively, some species maintain higher proportions of juveniles throughout the year which may be attributed to a still relatively high fecundity, slower maturation, and longer life spans (Turner et al. 1969). Species with longer life spans, later age at maturity and lower fecundity are characterized by population structures with almost equal proportions of adults and juveniles (Ballinger 1973, Stearns 1992). We propose that small populations are susceptible to disruptions of age or stage structure of both sexes (hereafter, demographic structure) as a result of landscape fragmentation. However, because of the interplay between life history, breeding phenology, and habitat affinity among species, effects of fragmentation should manifest differently for the different species in an ecological community.

The consequences of landscape fragmentation may be exacerbated in ecosystems that are naturally patchy and may affect the population dynamics or persistence of species adapted to living in patchy habitats (Ryberg et al. 2013, Ryberg et al. 2015). The Mescalero-Monahans Sandhills ecosystem, located in southeastern New Mexico and adjacent west Texas, overlying the Permian Basin, is comprised of ancient parabolic dunes maintained by wind, moving sand, and partially stabilized by *Quercus havardii* (shinnery oak; Hall and Goble 2008). The system is characterized by a patchy arrangement of open dune blowouts (bowl-shaped depressions formed when sand is blown against the leeward slope with vegetated arms extending around the sides) in a matrix of shinnery oak flats (Fitzgerald and Painter 2009, Ryberg et al. 2015). Networks of roads built for oil and gas development results in persistent landscape fragmentation (Smolensky and Fitzgerald

2011, Leavitt and Fitzgerald 2013; Fig. 1) and these fragmented areas have more compact soils, shallower slopes, and less shinnery oak, which are strong indicators of degraded dune blowout landforms in this habitat (Hibbitts et al. 2013). The lizard community in this system is composed of species ranging from widespread generalists to an endemic habitat specialist (Table 1). To date, much work has focused on *Sceloporus arenicolus* (dunes sagebrush lizard), an endemic habitat specialist threatened by loss and degradation of shinnery oak dunes. This habitat specialist requires dune blowouts, which are an emergent landform maintained by complex interactions among wind, sand, and the shinnery oak (Ryberg et al. 2015). While previous work has shown population dynamics of *S. arenicolus* are particularly sensitive to configuration and condition of the dune blowout landforms (Smolensky and Fitzgerald 2011, Ryberg et al. 2013, Ryberg et al. 2015), they are not the only species in this lizard community that may be impacted by fragmentation (Leavitt and Fitzgerald 2013).

Several studies have addressed the effects of landscape or habitat fragmentation on community composition, species presence, and gene flow (Driscoll 2004, Hoehn et al. 2007, Munguia-Vega et al. 2013). In some cases, fragmentation *per se* did not affect most species (Schutz and Driscoll 2008); other studies concluded fragmentation appeared to drive species loss and changes in abundance (Driscoll 2004, Russildi et al. 2016). Species loss can lead to disassembly of structured communities (Leavitt and Fitzgerald 2013). In the Mescalero-Monahans Sandhills ecosystem, there is a pattern of nested community structure in lizards throughout the ecosystem (Ryberg and Fitzgerald 2016). In fragmented areas, community structure is random compared to the nested structure of lizard communities in unfragmented areas (Leavitt and Fitzgerald 2013). Although these studies

provide important information on effects of fragmentation on community structure, we are not aware of any studies that have quantified the effects of fragmentation on the demographic structure of multiple lizard species in a community.

Here, we evaluate the effects of landscape fragmentation on capture rates and the demographic structure of species in a dune-dwelling lizard community. We predict that: 1) the specialist species will have lower capture rates in fragmented areas while generalist species capture rates will be similar across fragmented and unfragmented areas and 2) the demographic structure of the endemic specialist in fragmented areas will deviate strongly from that in unfragmented (control) areas, and 3) the demographic structure of generalist species will show no effect of fragmentation. This is the first empirical study we are aware of that describes and quantifies the demographic effects of fragmentation in a community of lizards. This work provides important insights into how landscape fragmentation disrupts population structure of ecological specialist species, and how species in ecological communities vary in their response to fragmentation.

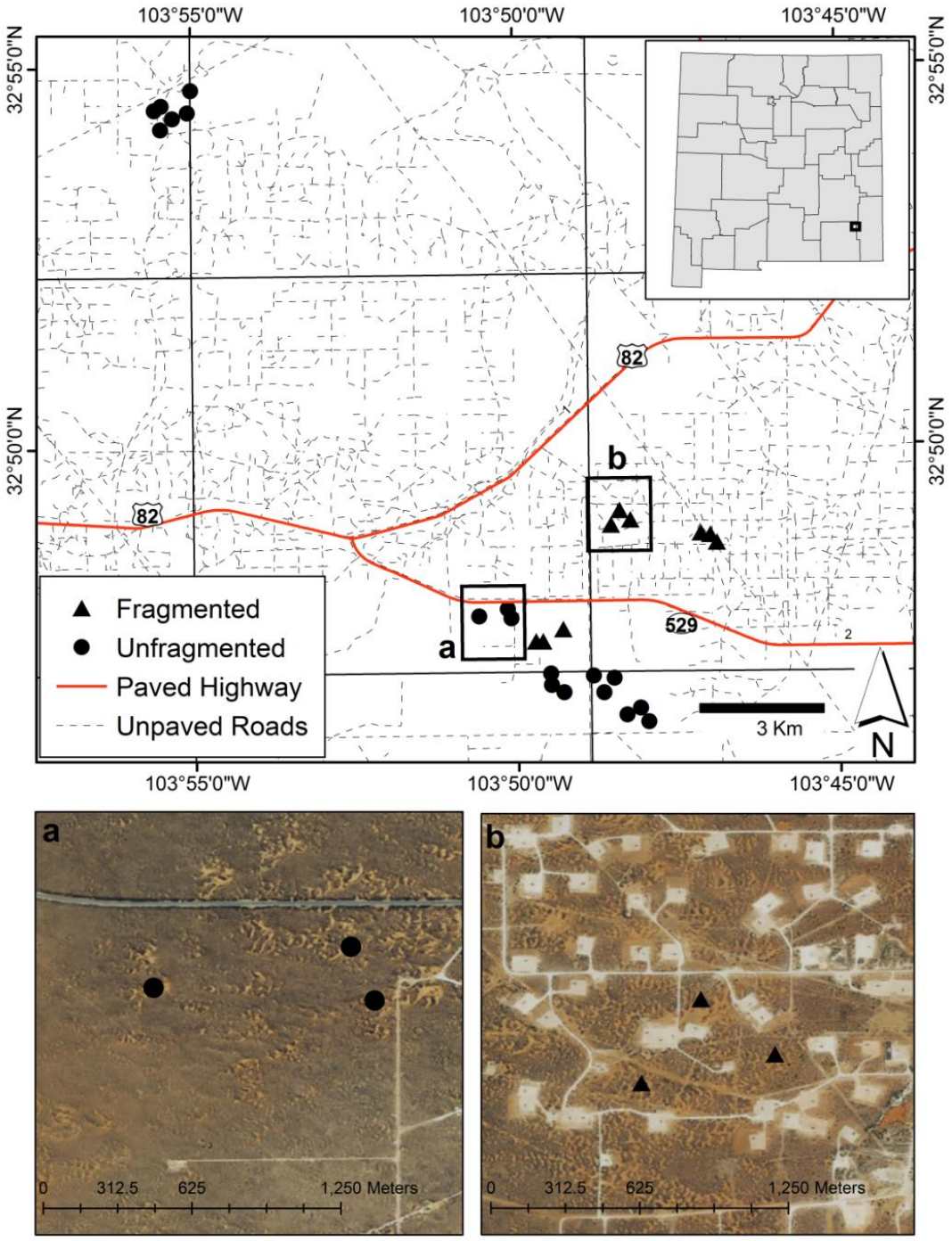

Figure 1 Map of the study area identifying the location of 27 trapping grids in southeastern New Mexico. The aerial images show trapping sites. Sites were classified as fragmented when the density of oil well pads was >13.0 well pads/section (259 ha). (a) An unfragmented site with one well pad and (b) a fragmented site with 61 well pads. Reprinted with permission from Walkup et al. 2017.

Table 1 Total captures and capture rates (mean captures/trap-day/grid) of eight species of lizard sampled on 27 trapping grids in unfragmented and fragmented sites during 2009-2013. Size at maturity, maximum size, and life span for females were estimated for the populations in our study area from our data unless otherwise indicated by superscripts. Reprinted with permission from Walkup et al. 2017.

Family Species	SVL at maturity (mm)	Max SVL (mm)	Clutch Size[†] (eggs per clutch)	Clutches per Season	Max Age (years)	Habitat Affinity[†]	Total Captures Capture rates ±SD	
							Unfragmented (n=18)	Fragmented (n=9)
Phrynosomatidae								
Holbrookia maculata	44[†]	75[†]	2.98-6.1	1-2[‡]	5[†]	**Generalist**: Grasslands Sand dunes	231 0.0045 ±0.0042	34 0.0012 ±0.0019
Phrynosoma cornutum	68[†]	86	23-30	>1[†]	10[†]	**Generalist**[§]: Deserts Grasslands Sand dunes	34 0.0006 ±0.0005	23 0.0008 ±0.0009
Sceloporus arenicolus	43	63	5.1	1-2[‡]	4[‡]	**Specialist**: Sand dunes	1,390 0.0148 ±0.0198	31 0.0011 ±0.0014
Sceloporus consobrinus	44	62	7.2-9.9	1-3[‡]	4[†]	**Generalist**: Woodlands Deserts Grasslands	173 0.0027 ±0.0022	59 0.0020 ±0.0016
Uta stansburiana	39	59	2-5	2-3[†]	3[†]	**Generalist**: Grasslands Woodlands Sand dunes	11,650 0.2028 ±0.0367	6,871 0.2356 ±0.0384

Table 1 Continued

Family Species	SVL at maturity (mm)	Max SVL (mm)	Clutch Size† (eggs per clutch)	Clutches per Season	Max Age (years)	Habitat Affinity†	Total Captures Capture rates ±SD	
							Unfragmented (n=18)	Fragmented (n=9)
Teiidae								
Aspidoscelis marmorata	69	98	2.2	1-2†	8†	**Generalist**: Woodlands Grassland Sand dunes	1012 0.0171 ±0.0114	508 0.0174 ±0.0128
Aspidoscelis sexlineata	54	81	2.9	1-2‡	4†	**Generalist**: Grasslands Deserts	168 0.0031 ±0.0011	90 0.0031 ±0.0008
Scincidae								
Plestiodon obsoletus	77	130†	12.3	0-1‡	8†	**Generalist**: Grasslands Riparian Woodlands	3 0.0001 ±0.0002	2 0.00007 ±0.0001

† (Degenhardt et al. 1996)
‡ (Jones and Lovich 2009)
§ Dietary Specialist

Methods

From May 2009 to September 2013, we trapped lizards on 27 pitfall grids in the Mescalero Sands ecosystem in Lea and Eddy Counties, New Mexico (Fig. 1). Nine grids were located in areas classified as fragmented treatments while another 18 grids were located in unfragmented areas as controls. Landscapes were classified as fragmented if there were 13 or more oil well pads in a section (259 ha), based on prior research that demonstrated a negative correlation between lizard densities and oil well density (Sias and Snell 1998, Leavitt 2012, Leavitt and Fitzgerald 2013). We selected this criterion for fragmentation because the value of 13 well pads per section has become implemented as a management threshold for conservation of *S. arenicolus* (Leavitt and Fitzgerald 2013). Well densities where the 18 unfragmented grids were located ranged from zero to 12.95 well-pads/section, and from 31.08 to 64.75 well-pads/section in fragmented treatments. The network of roads connecting well pads creates a grid-like pattern of fragmentation (Fig. 1b). Fragmentation can cause habitat degradation as well as loss of connectivity. Across sites in the Mescalero Sands ecosystem, the quality and quantity of shinnery dune habitat were significantly correlated (Smolensky and Fitzgerald 2011). Previous work also showed that fragmented sites had fewer, smaller and more dispersed dune blowouts than unfragmented sites (Leavitt and Fitzgerald 2013).

Pairwise distances among trapping grids ranged from 164 m to 19,054 m. The closest fragmented grids were 164 m apart and the closest unfragmented grids were 193 m apart. All other fragmented grids were > 235 m apart, while all other unfragmented grids were > 244 m apart. The nearest fragmented grid to an unfragmented grid was 806 m. All the trapping grids were located in shinnery oak dunes with blowouts that were known to be

occupied by *S. arenicolus* (Laurencio and Fitzgerald 2010). By design, the 27 independent sites were similar in landscape characteristics. The shinnery oak dune habitat that is required by *S. arenicolus* was similar among all trapping grids regardless of their spatial distribution and distances among them. This design allowed for statistically independent capture data, while testing for effects of landscape fragmentation in replicated similar habitat patches.

Each trapping grid consisted of 30 pitfall traps spaced 20 m apart in a 5x6 array, covering a total area of 1.2 ha. Traps were 20 L buckets buried with the rim level to the substrate with a 0.165 m^2 (16 in x 16 in) plywood cover. Sampling took place from May to August in 2009, from April to August in 2010, and from April to September in 2011-2013. Trapping grids were opened in four-day sessions. Each grid was opened for three sessions in 2009, and six sessions each in 2010 through 2013. This yielded a total of 9,720 trap-days in 2009 and 19,440 trap-days each season during 2010-2013.

For each lizard captured, we recorded species, trap number, sex, snout-vent length (SVL), and assigned a unique permanent mark by toe-clipping. We classified individuals as adult male, adult female, or juvenile based on sex and reported either the minimum SVL at reproductive maturity for each species or the smallest recorded gravid female in our data set (whichever was smaller; Table 1).

To calculate capture rates (captures/trap-day), species captures were standardized by trap days and stratified by treatment and year. Standardizing by capture rate controlled for differences in the number of trapping grids in unfragmented and fragmented sites. Although lizards were individually marked, we had very few captures on fragmented grids for some species (Table 1), and did not have enough recaptures on fragmented grids to use

capture-mark-recapture methods to test for differences in population abundances in unfragmented and fragmented sites. Thus we assumed that any difference in captures was dependent only on trapping effort, and used capture rates as a proxy for abundance. We tested for differences in mean capture rates by treatment and year for each species separately using two-way ANOVA. The arcsine transformation reduced heteroscedasticity and was appropriate given our question and the simple arrangement of yearly capture rates among treatments (Zar 1999). Significant interaction between treatment and year indicated whether species responded to annual environmental variability similarly in both treatments.

Monthly captures were pooled across years for each demographic then contingency tables were used to test the hypothesis of no difference in demographic structure of each species between fragmented and unfragmented treatments (Fitzgerald et al. 1999). We assumed that the frequencies of captures of each demographic on unfragmented sites represented the baseline demographic structure of the lizard populations in this ecosystem. Based on that assumption, we calculated the expected frequencies for captures of each demographic on fragmented grids, using the observed frequencies on unfragmented sites. Those expected frequencies were then tested against observed frequencies for the fragmented sites for the contingency tables. For *Uta stansburiana* (common side-blotched lizard) and *Aspidoscelis marmorata* (marbled whiptail), we subdivided the contingency tables and performed chi-square tests for differences in monthly proportions of each demographic on fragmented grids; the other species had such low frequencies (multiple cells with less than two expected captures) on fragmented grids each month that the assumptions of the chi-square test were violated and the tests were not performed (Fitzgerald et al. 1999, Zar 1999).

Results

From 2009 to 2013, we had a total of 22,279 captures of eight species of lizards. *Uta stansburiana* was the most common (18,521 total captures), followed by *A. marmorata* (1,520), and *S. arenicolus* (1,421). Three species, *Holbrookia maculata* (common lesser earless lizard), *Aspidoscelis sexlineata* (six-lined racerunner), and *Sceloporus consobrinus* (prairie lizard), were captured in much lower frequencies. We excluded *Phrynosoma cornutum* (Texas horned lizard) and *Plestiodon obsoletus* (Great Plains skink) from statistical analyses because of very few captures of these species (Table 1).

We observed statistically significant differences in annual mean capture rates in unfragmented and fragmented treatments for *U. stansburiana* ($F_{1,125} = 9.77$, $P < 0.01$), *S. arenicolus* ($F_{1,125} = 111.91$, $P < 0.01$), and *H. maculata* ($F_{1,125} = 25.70$, $P < 0.01$; Fig. 2). *Sceloporus arenicolus* and *H. maculata* were captured significantly more in unfragmented areas (unfragmented mean = 0.015, SD = 0.020; fragmented mean = 0.001, SD = 0.001, unfragmented mean = 0.005, SD = 0.004; fragmented mean = 0.001, SD = 0.002, respectively). Captures of the specialist *S. arenicolus* were remarkably low in the fragmented areas, with only 31 of 1,421 captures from five of the nine fragmented grids (range 1-11 individuals captured on each fragmented grid). We did not capture *S. arenicolus* on four of the nine fragmented grids in five years of trapping, despite deliberate placement of grids in close proximity to recent museum records of *S. arenicolus*. The generalist species, *U. stansburiana*, had higher capture rates in fragmented areas (fragmented mean = 0.24, SD = 0.04; unfragmented mean = 0.20, SD = 0.04). There were no differences in mean capture rates for *A. marmorata*, *A. sexlineata*, and *S. consobrinus*

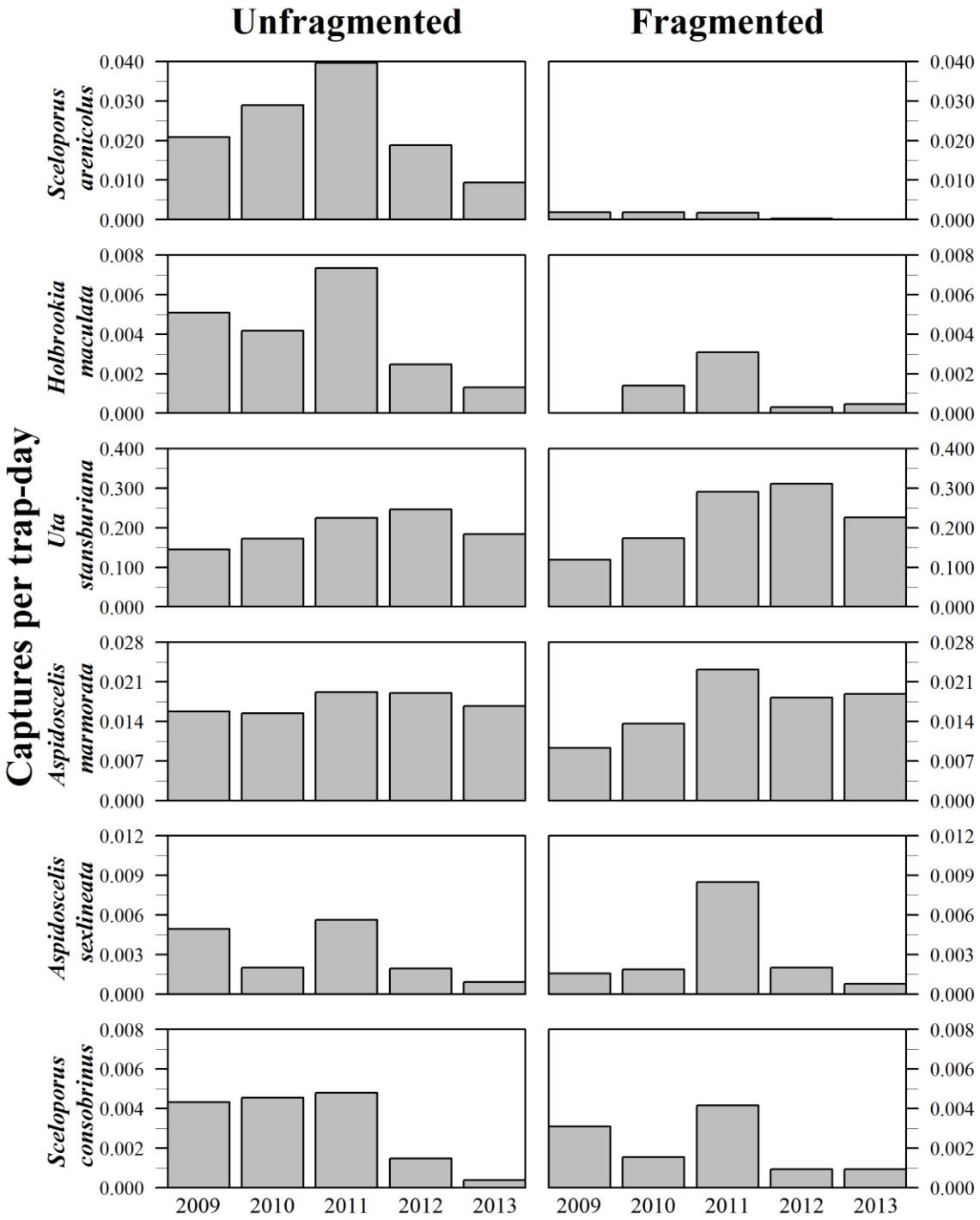

Figure 2 Yearly capture rates (captures/trap-days) for each species on unfragmented and fragmented trapping grids. The scale of the y-axis is different for each species relative to their abundance. Reprinted with permission from Walkup et al. 2017.

between treatments ($F_{1,125} = 0.14$, $P = 0.71$, $F_{1,125} = 1.04$, $P = 0.31$, $F_{1,125} = 0.96$, $P = 0.33$, respectively).

Capture rates varied significantly across years for *U. stansburiana* ($F_{4,125} = 36.47$, $P < 0.01$), *S. arenicolus* ($F_{4,125} = 6.23$, $P < 0.01$), *H. maculata* ($F_{4,125} = 5.89$, $P < 0.01$), *A. sexlineata* ($F_{4,125} = 16.73$, $P < 0.01$) and *S. consobrinus* ($F_{4,125} = 6.69$, $P < 0.01$; Fig. 2). The highest capture rates for these five species occurred in 2011, while the lowest capture rates occurred in 2013 for *S. arenicolus*, *H. maculata*, *S. consobrinus*, and *A. sexlineata* and in 2009 for *U. stansburiana*. *Aspidoscelis marmorata* capture rates did not vary significantly across years ($F_{4,125} = 1.43$, $P = 0.23$).

There was a significant statistical interaction between treatment (fragmented vs. unfragmented) and year for *U. stansburiana* ($F_{4,125} = 4.36$, $P < 0.01$) and *A. sexlineata* ($F_{4,125} = 3.24$, $P = 0.01$), revealing a pattern of inter-annual variation in capture rates among unfragmented and fragmented grids (Fig. 2). *Uta stansburiana* capture rates were higher on unfragmented grids than fragmented grids in 2009 and higher on fragmented grids 2010-2013. *Aspidoscelis sexlineata* capture rates were higher on unfragmented grids in 2009, 2012, and 2013 and higher on fragmented grids in 2010 and 2011. There was no interaction between year and treatment for the specialist *S. arenicolus*, nor for *H. maculata*, which were both significantly less numerous on fragmented grids ($F_{4,125} = 1.19$, $P = 0.32$ and $F_{4,125} = 1.38$, $P = 0.25$, respectively). There also was no significant interaction for *S. consobrinus* and *A. marmorata*, species that were not dependent on dune blowout landforms ($F_{4,125} = 0.84$, $P = 0.51$ and $F_{4,125} = 0.72$, $P = 0.58$, respectively).

Tests of contingency tables identified important differences in demographic proportions for some species (Fig. 3). Overall for *U. stansburiana*, significantly more

juveniles and fewer adults were captured on fragmented grids ($\chi^2 = 43.91$, df = 2, $P < 0.0001$). Subdivided contingency tables revealed significantly fewer adult females and more juveniles were captured in April and May ($\chi^2 = 53.40$, df = 2, $P < 0.0001$, and $\chi^2 = 79.69$, df = 2, $P < 0.0001$, respectively). In September, we captured significantly larger proportions of juveniles and smaller proportions of adult males ($\chi^2 = 12.37$, df = 2, $P = 0.0021$). There were no significant differences in demographic proportions for this species in June, July, and August on fragmented sites ($P > 0.05$).

The overall contingency table for *A. marmorata* showed there were significantly more juveniles and fewer adults captured on fragmented grids ($\chi^2 = 7.18$, df = 2, $P = 0.0276$; Fig. 3). The subdivided contingency table showed July had significantly fewer adult males and more juveniles ($\chi^2 = 7.03$, df = 2, $P = 0.0297$) and in August there were significantly more adult males ($\chi^2 = 6.64$, df = 2, $P = 0.0362$). There were no statistically significant differences in demographic proportions in April, May, June, and September ($P > 0.05$).

The contingency table for *S. arenicolus* showed there were significantly fewer adult males and more juveniles on fragmented sites ($\chi^2 = 6.15$, df = 2, $P = 0.0462$; Fig. 3). There were no significant differences in demographics for *H. maculata*, *S. consobrinus*, and *A. sexlineata* on fragmented and unfragmented grids ($\chi^2 = 1.25$, df = 2, $P = 0.5353$; $\chi^2 = 0.79$, df = 2, $P = 0.6737$; and $\chi^2 = 0.34$, df = 2, $P = 0.8437$, respectively).

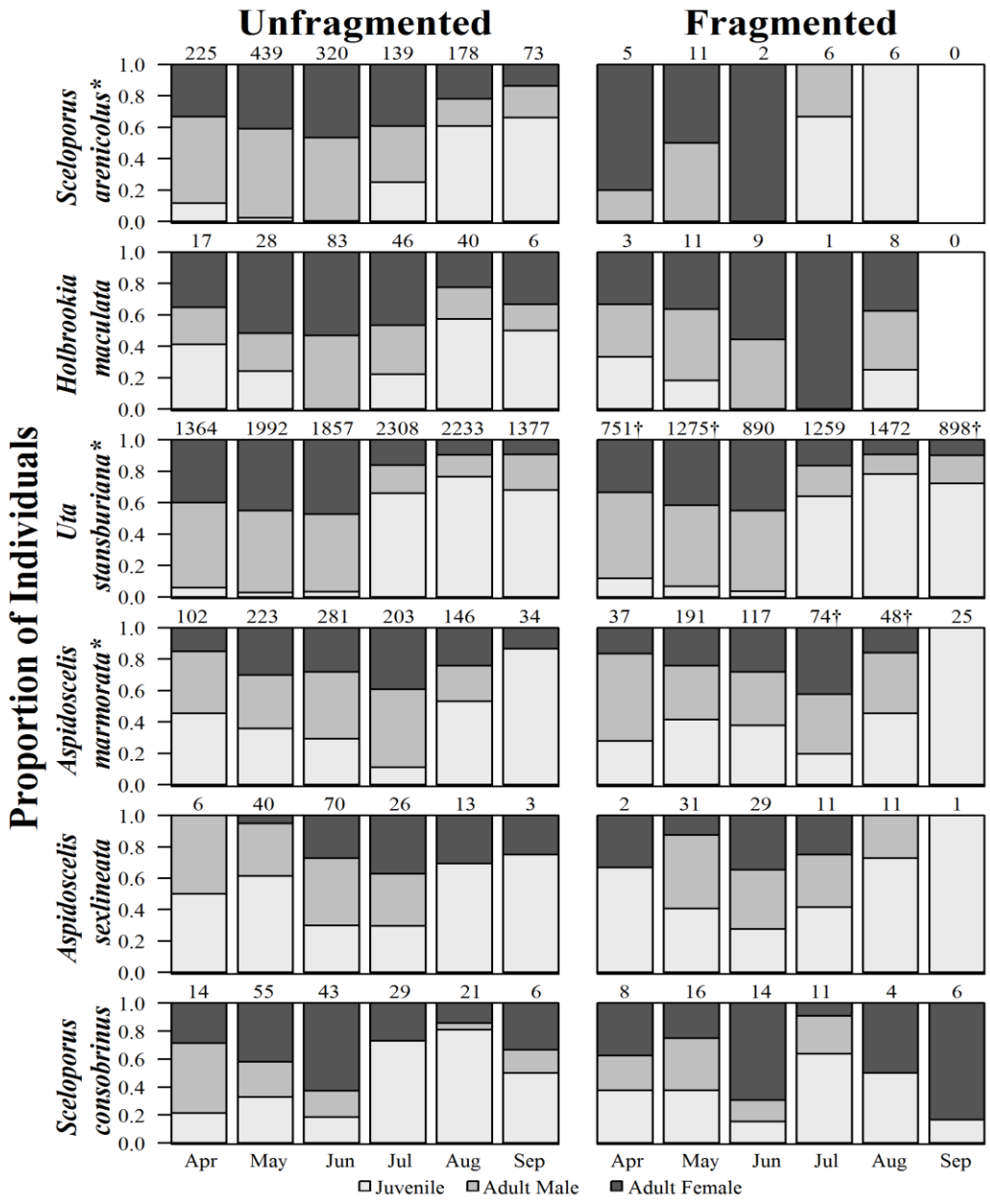

Figure 3 Demographic structures of each species on unfragmented and fragmented trapping grids from April to September, corresponding to the active season for lizards. Bars represent the proportion of juveniles, adult males, and adult females captured each month, with all five years of sampling combined, sample sizes for each month are above the bars. The asterisk (*) next to the species name indicates that on the fragmented grids that population had significantly different overall demographic proportions than expected compared to the baseline unfragmented grids. The dagger (†) next to the monthly sample sizes for *Uta stansburiana* and *Aspidoscelis marmorata* indicates that on the fragmented grids that population had significantly different demographic proportions that month than expected compared to the baseline unfragmented grids. Reprinted with permission from Walkup et al. 2017.

Discussion

Our results strongly supported our predictions and those of Andrén et al. (1997) and Henle et al. (2004) that species with the strongest habitat preferences should show the greatest response to landscape fragmentation. While the habitat specialist was strongly affected by fragmentation, with negative consequences for both abundance and demographic structure, we also showed generalist species exhibited a range of responses to fragmentation. Some generalists responded negatively, in particular *H. maculata*, while others appeared to prosper, namely *U. stansburiana* and *A. marmorata*. A similar pattern was described by Vega et al. (2000), who showed strong reduction in habitat area and population density in a habitat specialist lizard following construction of a road through coastal dunes and little response by the generalists.

The endemic and threatened habitat specialist, *S. arenicolus* merits careful discussion, because it lends insight as to how specialist species are affected by isolation and habitat degradation following fragmentation. *Sceloporus arenicolus* disappeared from fragmented sites and its demographic structure was clearly disrupted compared to unfragmented sites, where we observed a typically structured sequence of demographic cohorts across months during all sample years. Capture rates of *S. arenicolus* were very low on fragmented sites compared to unfragmented sites, and consistently declined across the five years of trapping, until we captured no *S. arenicolus* on any fragmented grid in the final year of the project. Meanwhile, in the 18 unfragmented sites, capture rates of *S. arenicolus* increased from 2009 to 2011 then decreased from 2011 to 2013, a pattern that was not statistically significant and was not unexpected for healthy fluctuating populations. There was at least one demographic life stage (adult males, adult females, or juveniles)

missing each month overall, and in each of the five seasons of the study. The demographic structure was skewed towards females on fragmented grids, albeit with few captures. We did not capture adults later in the trapping periods, with males captured only during April through June, and females captured in April, May and July. Young-of-year were not captured during April to May on fragmented sites, so it is reasonable to assume juveniles from the prior reproductive season on fragmented sites either emigrated or died. While low numbers on the fragmented grids could play some role in our ability to accurately assess demographic structure of *S. arenicolus*, we are confident, given the five years of intensive trapping, these results strongly suggest this specialist species has a relatively high susceptibility to local extinction following fragmentation. Taken together, we interpret these results to mean there were too few *S. arenicolus* on fragmented grids necessary to maintain the demographic structure of a self-sustaining population (Fig. 2; Fig. 3).

We also documented significantly fewer captures and disrupted demographic structure in *H. maculata* in the fragmented sites, indicating the changed landscape of the fragmented treatments had a detrimental effect on their populations. For example, on fragmented grids, only males were captured in July, where we expected to capture adult females and hatchlings as well. Also, we captured no *H. maculata* in September on fragmented grids despite having captured them on unfragmented grids during this month. In this ecosystem, *H. maculata* occurs along roads, basks on roads, and uses several vegetation types in sandy areas (Degenhardt et al. 1996). It remains unclear why this species should be susceptible to fragmentation. Leavitt and Fitzgerald (2013) examined the effects of changes in habitat structure on community structure in this system and also found *S. arenicolus* and *H. maculata* were sensitive to fragmentation and consistently were

the first two species to disappear from fragmented sites. Leavitt (2012) showed the abundances of these two species were not associated with the same landscape features. *Sceloporus arenicolus* abundance was associated with steep slopes and relatively hard soils, while *H. maculata* abundance was positively associated with flat slopes and relatively hard soils, suggesting they were affected by fragmentation for different reasons. Even though the mechanisms of how these species responded to fragmentation may have differed, their populations showed similar patterns of demographic disruption.

The super-abundant (18,521 captures) short-lived generalist, *U. stansburiana*, had both higher capture rates and more variable demographics in fragmented areas. Capture rates were higher in unfragmented grids in some years, and higher in fragmented grids in others. Our interpretation of this significant interaction between year and treatment pattern was that stochastic responses to the environment among years in this abundant, short-lived generalist varied locally and was not strongly influenced by fragmentation. On the fragmented grids there were more juveniles captured than expected in April, May, and September with all years combined.

Aspidoscelis marmorata capture rates were consistent across treatments and showed no effect of inter-annual variation. This species is longer lived than the other generalist species, uses many habitats, and is also the most wide-ranging, active forager in this lizard community. Despite the generalist nature of *A. marmorata*, contingency tests revealed juveniles were captured at significantly higher frequencies than expected on fragmented grids in July and August. These differences later in the breeding season may have resulted from either more nesting in the fragmented areas or hatchlings having higher survival rates in fragmented areas.

Two generalists, *S. consobrinus* and *A. sexlineata*, both with relatively moderate life spans, moderate body sizes, and moderate to high fecundity, showed no significant differences in the demographic structure at unfragmented and fragmented sites. In addition, *S. consobrinus* showed no significant response in capture rates by year or treatment. The lack of response by this species is consistent with predictions; in this area *S. consobrinus* tends to use only the extensive matrix of shinnery oak flats surrounding dune areas. *Aspidoscelis sexlineata* is a wide-ranging active forager that occurs within and outside dunes, similar in life history to its congener *A. marmorata.* Although for *A. sexlineata* we found a significant year-by-treatment interaction in capture rates (with higher capture rates on fragmented grids in 2010-2011), there were no clear differences between fragmented and unfragmented treatments. In the end, it is likely these two species, which use habitats surrounding the dunes were less affected by fragmentation.

The variable response seen among these five generalist species in this lizard community can be at least partly explained by differences in habitat affinity, breeding phenology, and life history of the species (Fitzgerald et al. 1999). For example, the pattern in the demographic structure of *U. stansburiana* (a small, short-lived, highly fecund phrynosomatid) reflected its breeding phenology. There were high proportions of juveniles in July through September after emergence of abundant hatchlings, and very low proportions of juveniles the next spring, as the young grew quickly to adult size. In contrast, in *S. consobrinus* and *H. maculata* (phrynosomatids that are larger and longer lived, with relatively high fecundity) we observed high proportions of juveniles during a prolonged breeding season, which we attributed to their relatively high fecundity and longer life spans. Finally, the active-foraging teiids *A. marmorata* and *A. sexlineata* are

larger, longer lived, and slower maturing than other species in this assemblage. Their life history and breeding phenology helps explain why we observed juveniles of these species throughout the activity season, as young continue to grow to adult size throughout the following year. Two species whose life history strategies were considered intermediate, *S. consobrinus* and *A. sexlineata*, showed no changes in either capture rates or demographic structure in fragmented sites. Finally, the two species on the opposite end of the life history gradients among the species we studied, *U. stansburiana* (short-lived, habitat generalist) and *A. marmorata* (long-lived, large, wide-ranging forager), appeared to benefit at the fragmented sites.

Although the effects of habitat loss and fragmentation are tightly intertwined, studies that have tried to isolate the effects of both of these landscape changes have found habitat loss generally has a stronger effect on populations than does habitat fragmentation *per se* (Fahrig 1997). In our study system, the network-like development of well-pads and their connecting roads both isolates populations and disrupts the underlying geomorphologic processes that maintain the shinnery oak dune blowout formations (Ryberg et al. 2015). In comparison to other drivers of fragmentation, such as deforestation, this road-network type of fragmentation directly converts a relatively smaller percentage of the landscape surface (e.g., Smolensky and Fitzgerald 2011), but drives processes that result in large-scale degradation of irreplaceable landforms on which the habitat specialist depends (Ryberg et al. 2015). Accordingly, we believe the disrupted demography and declines observed in *S. arenicolus* and *H. maculata* were driven by the effect of fragmentation on landscape integrity and habitat quality.

Fragmentation theory has previously treated the matrix of vegetation that lies between habitat patches as an inhospitable ocean (i.e., patch-isolation model), but more recently a viewpoint has emerged that there is a continuum of matrix and patch-level configurations (Didham et al. 2012). In the case of the Mescalero-Monahans Sandhills ecosystem, it has been demonstrated that the extensive network of roads and well pads degrades the dune blowout landform, changes landscape configuration, and isolates patches of shinnery oak dunes (Hibbitts et al. 2013, Leavitt and Fitzgerald 2013, Ryberg et al. 2015). As such, for species like *S. arenicolus* that have very specific habitat requirements, the concept of the inhospitable matrix may be more relevant. *Sceloporus arenicolus* occurs only in and around interconnected blowouts in relatively large expanses of shinnery oak dunes (Fitzgerald and Painter 2009, Laurencio and Fitzgerald 2010). Movements among disconnected patches have never been observed. This study gives insight into the mechanism of how fragmentation results in disruption of demographic structure in isolated populations of *S. arenicolus*. Previous studies of this habitat specialist showed that areas of poor dune quality were population sinks. Persistence in poor quality habitat relied on diffusion dispersal of juveniles through interconnected dune blowouts to offset the imbalance between natality and mortality in sink neighborhoods (Ryberg et al. 2013). Landscape condition, which is negatively affected by fragmentation, and population impacts go hand-in-hand. There are tight linkages between condition of shinnery dune blowouts and vital rates of *S. arenicolus*; elasticities in adult survival, juvenile survival, and fertility of *S. arenicolus* were strongly and significantly associated with fractal dimension of interconnected dune blowouts (Ryberg et al. 2015). Moreover, fragmentation of the shinnery dune landscape leads to disassembly of the entire lizard community, largely

because of the loss of the habitat specialist (Leavitt and Fitzgerald 2013). The incredibly low capture rates we observed in isolated fragmented sites compared to unfragmented sites over five years reflects the disruption of demographic structure in populations that have become isolated with no rescue effect from immigration. The end result for small, isolated populations of *S. arenicolus* is localized extinctions.

This study also lends insight into the linkages between disturbance of landscape features and the consequences for populations. In short, fragmentation disrupts both the landscape features and the lizard populations. This is the first study to link empirically derived patterns of demographic structure to landscape fragmentation in a lizard community that contains specialist and generalist species. We were able to make direct comparisons of population structure at unfragmented and fragmented sites, and we demonstrated deterioration of demographic structure could be a sign of impending extirpation of species affected by fragmentation. As such, this study enhances previous work on the effects of fragmentation on this lizard community, and demonstrates how populations that are sensitive to fragmentation may begin to deteriorate through the loss of specific components (adult males, adult females, or juveniles) of their population structure. Future work could build on the relationships we have drawn between life history traits and habitat affinity of species, and how these may serve as predictors of how species may respond to fragmentation. This research enhances the picture of how fragmentation may cause demographic disruption and decline of some species while having little effect on others.

CHAPTER III

MICROHABITAT USE AND LANDSCAPE CONTEXT DETERMINE SPATIAL SETTLEMENT AND VACANCY DYNAMICS IN AN ENDEMIC HABITAT SPECIALIST

Synopsis

The distribution of individuals in landscapes over time affects population dynamics and persistence of species. Understanding how species are distributed throughout their habitats requires understanding the hierarchy of habitat selection made by individuals, the resulting spatio-temporal structure of demography, and the consequent dynamics of localized populations. This study looks to fill gaps in understanding how patterns of use, settlement, and vacancy of an endemic habitat specialist, *Sceloporus arenicolus* (dunes sagebrush lizard), may be affected by habitat at the microscale, which varies in configuration within the larger landscape-scale context, in the Mescalero Mohanans Sandhills ecosystem. To understand these patterns, we developed models to identify determinants of use, settlement, and vacancy at both the microhabitat and larger landscape scales at two different sites. For each site individually, we modeled use, settlement, vacancy, and detection as functions of microhabitat and landscape variables in separate analyses. Our study showed that microhabitat and landscape context influence use, settlement, and vacancy patterns in complex ways. Microhabitat variables better predicted the probability of use, while landscape-scale variables better predicted probabilities of settlement and vacancy. Use, settlement, and vacancy patterns in *S. arenicolus* populations were dynamic, and no single variable consistently predicted these dynamics. The

configuration of landscape features, in particular the arrangement of shinnery dune blowouts, is important for the maintenance of populations of *S. arenicolus*. Indeed, maintaining connectivity of dune blowouts is the best way to ensure persistence of *S. arenicolus* populations by allowing them to maintain settlement and vacancy dynamics across the landscape. Both microhabitat and landscape variables determine how this species uses, moves through, and occupies habitat through time.

Introduction

Understanding how the distribution of individuals in landscapes over time affects population dynamics and persistence is an overarching question in ecology (Turner and Chapman 2005). Even continuous habitats are not usually homogenous but can be made up of a mosaic of patches of resources (Merriam 1995, Shaver 2005). The configuration of these mosaics of varying quality influences species' distributions through patterns of dispersal of individuals, populations, and species across landscapes over time (González-Megías 2005, Turner and Chapin 2005, Ryberg et al. 2013). Understanding how a species is distributed across the landscape is especially important in conservation contexts, as variations in habitat quality can drive population persistence in patchy landscapes (Ye et al. 2013a, b).

Understanding how species are distributed throughout their habitats requires understanding the hierarchical use of habitat by the animal (Levin 1992, Wiens et al. 1993). Because the movements of individuals scale up to broader patterns of occupancy and distribution, understanding distribution patterns at smaller scales can be helpful in understanding the scalar nature of habitat use and inform conservation aims (Wiens et al. 1993). Both local landscape variables (microhabitat) and larger landscape patterns

(macrohabitat) influence the dynamics of how individuals move and settle among different quality habitats (Frey et al. 2012, Herse et al. 2017). While macrohabitat characteristics are perhaps more easily understood and more often considered, microhabitat characteristics add important information and improve predictions of population parameters such as density, abundance, and occupancy (Cornell and Donovan 2010, McClure et al. 2012). For example, Michael et al. (2017) showed that both local and landscape scale variables were important for predicting the occupancy of many reptile species in a woodland-agriculture matrix. Many important population processes (e.g., density, recruitment) are local in scale, but vary over time and space (Krohne and Burgin 1990).

This study looks to fill in gaps in understanding how patterns of use, settlement, and vacancy of a habitat specialist may be affected by habitat at the microscale, which varies in configuration within the larger landscape-scale context. *Sceloporus arenicolus* (dunes sagebrush lizard) is a habitat specialist endemic to the Mescalero Monahans Sandhills ecosystem of West Texas and southeast New Mexico. Because of the well understood pattern of hierarchical scaling of habitat use in this system, it is excellent for studies on how movements and distribution are constrained by the configuration of specific habitat features at multiple scales. At the regional scale, we know that *S. arenicolus* is found only in the Mescalero Monahans Sandhills ecosystem (Fitzgerald et al. 1997, 2011; Laurencio et al. 2007; Laurencio and Fitzgerald 2010). Within this ecosystem, *S. arenicolus* exclusively uses the mosaic of dune blowouts in the shinnery oak (*Quercus havardii*) matrix (Fitzgerald and Painter 2009). At the local scale, *S. arenicolus* select larger blowouts with steeper slopes, lower substrate compaction, medium sand grain sizes, and less vegetative cover (Fitzgerald et al. 1997, Smolensky and Fitzgerald 2011, Hibbitts

et al. 2013). *Sceloporus arenicolus* are spatially distributed in neighborhoods (*sensu* Addicott 1987, localized groups of interacting individuals within a continuously distributed population; Ryberg et al. 2013) and survivorship and fecundity in neighborhoods were tightly linked to habitat configuration. However, these associations of habitat use are snapshots and we do not have a longer term understanding of how landscape features influence *S. arenicolus* movements. Even in areas considered highly likely to contain *S. arenicolus*, they show a patchy distribution, and there are areas in the dune blowout landscape where we expect to find them and do not (Walkup et al. In Review, Fitzgerald et al. 1997). This study looks to fill in gaps in understanding how use, settlement, and vacancy are affected by habitat at the microscale and within the larger landscape context.

To gain insight into these questions, we developed models to understand landscape determinants of use, settlement, and vacancy at both the microhabitat and larger landscape scales. Using both microhabitat variables and landscape variables in our models should help clarify which scale better predicts *S. arenicolus* distribution and temporal dynamics. Incorporating the dynamics of settlement and vacancy along with use should allow us to predict features of areas that should be constantly occupied, intermittently used, or not used at all. Given the dynamic landscape they occupy, we predict that *S. arenicolus* use, settlement, and vacancy will respond dynamically over time to different microhabitat and landscape features (i.e. there is not one specific feature of the landscape that will consistently best predict the model parameters). We also predict that the microhabitat variables that *S. arenicolus* uses will scale correspondingly to the landscape features (i.e. selection of percent cover of sand at the microscale will correspond with selection of large sand patch areas at the landscape scale). Finally, we predict that both the microhabitat and

landscape scales will be important for understanding use, settlement, and vacancy of *S. arenicolus* over the landscape.

Methods

Trapping

Two large trapping arrays, each covering 13.69 ha, were installed in May 2012. Each 6 x 6 array consisted of 36 sub-grids spaced 50 m apart. The 36 sub-grids were 3 x 3 pitfall trap arrays with the traps spaced 10 m apart (Fig. 4). One array was in disturbed habitat with 3 oil well-pads in and around it and a road cutting through it. The other array was in relatively undisturbed habitat. On the disturbed site, three sub-grids in the bottom right corner were eliminated because a well-pad was installed in that area over winter of 2012 (Fig. 4B). Traps were 20-l buckets buried with the rims flush to the ground, with 40cm x 40cm plywood cover boards propped over them 1-2 inches high (Fitzgerald 2012). We sampled from April through August 2012-2015. Each trapping session lasted 7 days in 2012 and 5 days in 2013-2015. There were 5 trap sessions during May-August 2012. With the 5-day trapping periods, we were able to increase the number of sessions to 9 each during April-August 2013-2015. Traps were checked and cleared every 24 hours.

Microhabitat Variables

Microhabitat variables were measured at each trap in 2014: slope (degrees); substrate compaction (brand and model of penetrometer); and percent cover for 6 cover types (sand, shinnery oak, yucca/shrubs, forbs/ grasses, caliche, and litter). The microhabitat data were averaged for each sub-grid and a Principal Components Analysis

Figure 4 *Sceloporus arenicolus* trapping sites in Andrews County, Texas. (A.) Both sites in the landscapes: disturbed site on the left, undisturbed on the right, (B) disturbed site, (C) undisturbed site.

(PCA) using the covariance matrix was used to reduce the dimensionality and identify the main sources of variation for the microhabitat in each sub-grid. The data were transformed using log transformations (slope and penetrometer) or arc-sine transformations (percent cover variables) to better meet normality assumptions of the test (Gotelli and Ellison 2004). The first two PCA axis scores were then used as independent variables in subsequent analyses.

Landscape Variables

A supervised classification of 1-m resolution NAIP imagery was used to determine five cover classes (sand, shinnery oak, mesquite, grass, and caliche) across *S. arenicolus*' range in Texas, creating a raster for each class. For the purposes of this study, we clipped these rasters with a 35 m buffer around each site. Because the sand and caliche classes are hard to distinguish between using their spectral reflectance, these two cover classes were merged and considered sand. To get the caliche cover class, polygons were hand drawn covering roads and well-pads and merged into the raster, leaving us with five cover classes: sand, shinnery oak, mesquite, grass, and road- well pad. These rasters were divided into a six by six grid, creating 36 landscapes, each centered on one of the trapping sub-grids and encompassing 70 m x 70 m.

We used Fragstats v. 4.2 to estimate class metrics for each landscape: mean patch size (ha) for sand, shinnery oak, and the road- well pad cover layers; total edge for the sand, shinnery oak, and the road- well pad cover layers; fractal dimension for the sand and shinnery oak cover layers, and clumpiness index for the sand and shinnery oak cover layers. Fractal dimension reflects the mean shape complexity of patches in each cover class on a scale of 1, where the mean focal patch is an Euclidean shape, like a square or circle, to

2, where the mean focal patch has a highly convoluted perimeter (Turner 1990). The clumpiness index measures the mean degree of aggregation of patches in each cover class across the landscape on a scale of -1, where the focal patch is maximally disaggregated, to 1, where the focal class is maximally aggregated. These class metrics were chosen because previous research has shown that metrics of these types have some predictive value for *S. arenicolus* population parameters (Ryberg et al. 2013, 2015). Total edge was removed after doing a correlation matrix because it was highly correlated with all other variables. Finally, a Principal Components Analysis (PCA) was used to reduce the dimensionality and identify the main sources of variation for the landscape in each site.

Modeling

We used the approach developed by MacKenzie et al. (2003) for dynamic occupancy modeling to estimate patterns of settlement and vacancy in the microhabitat and local landscape of the sampling arrays. Because we are measuring patterns of how microhabitat influences distribution of individuals across landscapes in two continuous populations, our model estimates are best expressed as use, settlement, and vacancy (following Efford and Dawson 2012, Betts et al. 2008, McClure and Hill, 2012). Trap data were aggregated into a presence-absence matrix for each sub-grid. Each trap session was considered a "season" and the trap days were the repeat surveys in order to better meet the assumption of closure. Then, each sample year (2012-2015) was analyzed separately because of the 6-month interval without trapping between each breeding season.

We developed multiple models to understand relationships of both microhabitat and landscape variables. For each site, individually, we modeled use, settlement, vacancy, and detection as functions of the PCA axis scores for microhabitat and landscape variables;

the microhabitat and landscape variables were included in separate analyses. We also included each trapping occasion as a time covariate for settlement, vacancy, and detection. Finally, we included an autocovariate to account for the influence of spatial autocorrelation of *S. arenicolus* detections in our models. We modeled this as $AUTO_i = \sum W_{ij} Y_j / \sum W_{ij}$ where W_{ij} = the inverse geographic distance between sub-grids i and j and Y_j = the presence of *S. arenicolus* in sub-grid j (i.e. 1 if present, 0 if absent) (Augustin et al. 1996, Betts et al. 2006, Chammem et al. 2012). This autocovariate gives us an index from 0 (none of the surrounding sub-grids are occupied) to 1 (all of the surrounding sub-grids are occupied) for each of the sub-grids in each trapping occasion.

Results

Trapping

Over the four years of trapping (2012-15), the two arrays were operational for 125,712 trap-days (2012, n = 26,568; 2013, n = 33,048; 2014, n = 35,640; 2015, n = 30,456). During this time, we captured 12,814 lizards of 8 species, of which 1,539 were *S. arenicolus*. These numbers include repeated captures of the same individuals. After creating capture histories for individual lizards, 726 unique individual *S. arenicolus* were captured: 549 on the undisturbed site and 177 on the disturbed site. Of the total 813 recaptures, 681 on the undisturbed site and 132 were on the disturbed site. Detections at each grid within the sites varied from year to year, with more detections on the undisturbed site than on the disturbed site (Table 2).

Table 2 Detections of *Sceloporus arenicolus* on the undisturbed and disturbed site over four years of trapping. Detections indicate presence and absence of *S. arenicolus* for all trapping grids within each site over all the days of trapping. Naïve occupancy is the number of trapping grids on which S. arenicolus were found compared to the total number of grids at each site.

	Undisturbed Site		Disturbed Site	
	Detections (Present/Absent)	Naïve Occupancy (Occupied/Total)	Detections (Present/Absent)	Naïve Occupancy (Occupied/Total)
Year 1	130/1130	21/36	32/1123	11/33
Year 2	260/1360	24/36	53/1432	17/33
Year 3	215/1405	22/36	56/1429	15/33
Year 4	198/1422	20/36	104/1381	16/33

Microhabitat Principal Components Analysis

The first two PC axes explained 57.2 and 18.4 percent of the variation in microhabitat on the undisturbed site, and 50.6 and 24.5 percent of the variation on the disturbed sites (Table 3). These axis scores were used as independent covariates in the settlement and vacancy models. On both the undisturbed and disturbed sites, the first PC axis represented a slope and compaction gradient, where higher average slopes corresponded with lower average compaction values (UM1 and DM1, respectively). Larger dunes with steeper slopes tend to have looser sand, which makes for a less compact substrate, while the flatter areas correspond with the more compact mesquite (*Prosopis glandulosa*) grassland and caliche. On the undisturbed site, the second PC axis (UM2) captured a gradient of high to low percent shinnery oak and percent litter cover. On the disturbed site, the second PC axis (DM2) also captured variation in the cover types, with percent sand cover on one end of the gradient and percent shinnery oak and percent litter cover on the other. Since shinnery oak is the densest vegetation on our sites, this likely represented a cover gradient from dense vegetation to the more open sandy areas.

Table 3 Results of the principal components analyses for the Microhabitat and Landscape variables on the undisturbed and disturbed sites. Only the top two principal component axes were retained from each analysis.

		Undisturbed (N = 36)		Disturbed (N = 33)	
	Variable	PC1	PC2	PC1	PC2
Microhabitat	Mean Slope	0.6298	0.6215	-0.5949	0.1366
	Mean Compaction	-0.6601	0.3411	0.7281	0.3740
	% Cover Sand	0.2241	0.2140	-0.2346	0.5710
	% Cover Shinnery Oak	0.2109	-0.5058	-0.0437	-0.5432
	% Cover Caliche	-0.2475	0.3234	0.0706	0.2117
	% Cover Grass/Forb	-0.1001	0.2944	0.0580	-0.0627
	% Cover Shrub/Yucca	0.0400	0.0506	0.0397	-0.0123
	% Cover Litter/Other	0.0030	-0.0444	0.2215	-0.4141
	% Variance Explained	59.1	16.0	50.6	24.5
Landscape	Mean Patch Area Sand	0.6091	-0.2750	0.6149	0.0632
	Mean Patch Area Shinnery Oak	-0.1077	0.6882	-0.4343	0.0253
	Mean Patch Area Road- well pad	NA	NA	0.4199	-0.0675
	Fractal Dimension Sand	0.3683	0.3195	0.3311	0.6458
	Fractal Dimension Shinnery Oak	0.3245	0.5810	-0.0930	0.6339
	Clumpiness Sand	0.5911	-0.1008	0.3725	-0.4146
	Clumpiness Shinnery Oak	0.1646	-0.0303	NA	NA
	% Variance Explained	29.3	26.2	35.0	21.7

Landscape Principal Components Analysis

The first two PC axes explained 29.3 and 26.2 percent of the variance in landscape configuration on the undisturbed site respectively and were retained as covariates in the models (Table 3). On the undisturbed site, the first PC axis (UL1) represented a gradient from large, aggregated sand patches to small, more dispersed sand patches. On the undisturbed site, the second PC axis (UL2) captured a gradient of large areas of shinnery oak corresponding with high fractal dimensions for the shinnery oak patches, indicating a gradient from larger, complex shinnery oak patches to smaller, simpler shinnery oak patches. On the disturbed site the first two PC axes explained 35.0 and 21.7 percent of the variance in landscape configuration, respectively (Table 3). The first PC axis (DL1)

represented a gradient where large areas of sand and patches of caliche for roads and well pads contrasted with large patches of shinnery oak, indicating that the sand and road-well pad patches dominated in some areas, while shinnery oak patches dominated others. On the disturbed site, the second PC axis (DL2) captured a gradient of larger fractal dimensions of sand and oak patches contrasted with high clumpiness values for sand patches, indicating that the more highly aggregated sand patches had less complex patch shape, and that complex shapes of sand patches correlated with complex shapes of shinnery oak patches.

Models

Detection

For the microhabitat models, on the undisturbed site, detection probability was best explained by the slope-compaction gradient in all four years; detection probability increased as the mean slope of blowouts increased. We also saw an additive time effect on detection probability in years 1 and 3, with variation among years as to which sessions had the highest detection probability (Table 4). On the disturbed site, detection probability was more variable than on the undisturbed site (Table 4). In year 1, detection probability was constant ($p = 0.12 \pm 0.03$ SE). In years 2 and 3, detection probability increased as the mean slope increased. Detection probability in year 2 also had an additive effect from the autocovariate, where detection probability increased as the percentage of occupied surrounding sites increased. Finally, in year 4, detection probability increased slightly as percent sand cover increased.

For the landscape-scale models, we found considerable variation in which covariates best predicted detection probability (Table 4). On the undisturbed site, for year 1, a counter-intuitive pattern emerged. Detection probability decreased as the percentage of

Table 4 Covariates from each of the top models for the microhabitat and landscape dynamic occupancy models from the undisturbed and disturbed sites. Model covariates are: (.) = constant model; A = autocovariate; DL1 = disturbed landscape PC axis 1 - large shinnery oak patches to large sand and road-well pad patches gradient; DL2 = disturbed landscape PC axis 2 - highly aggregated sand patches to complex sand and shinnery oak patches gradient; DM1 = disturbed microhabitat PC axis 1 - high average slope to high average compaction gradient; DM2 = disturbed microhabitat PC axis 2 - high oak and litter cover to high sand cover gradient; S = Session (time effect); UL1 = undisturbed landscape PC axis 1 - large, aggregated sand patches to small, disaggregated sand patches gradient; UL2 = undisturbed landscape PC axis 2 - large, complex shinnery oak patches to small, simple shinnery oak patches gradient; UM1 = undisturbed microhabitat PC axis 1 - high average slope to high average compaction gradient; UM2 = undisturbed landscape PC axis 2 - high to low percent cover of oak and litter gradient; NE = Not Estimable.

		Year	Use	Settlement	Vacancy	Detection
Microhabitat	Undisturbed	1	ψ(UM1)	γ(.)	NE	*p*(UM1+S)
		2	ψ(UM2)	γ(S)	ε(UM2+S)	*p*(UM1)
		3	ψ(UM2)	γ(UM1)	NE	*p*(UM1+S)
		4	ψ(UM1)	γ(A)	ε(UM1)	*p*(UM1)
	Disturbed	1	ψ(DM2)	γ(.)	NE	*p*(.)
		2	ψ(DM1)	NE	ε(DM1+A)	*p*(DM1+A)
		3	ψ(.)	γ(DM2)	NE	*p*(DM1)
		4	ψ(DM2)	γ(DM1+S)	NE	*p*(DM2)
Landscape	Undisturbed	1	ψ(.)	γ(A+S)	NE	*p*(A+S)
		2	ψ(.)	γ(UL1+A)	ε(UL2)	*p*(UL1+S)
		3	ψ(UL1)*	γ(A)	ε(UL2+A)	*p*(UL2+S)
		4	ψ(UL2)	γ(A)	ε(.)	*p*(UL1)
	Disturbed	1	ψ(.)	γ(DL1)	NE	*p*(DL1)
		2	ψ(.)	γ(.)	ε(.)	*p*(A)
		3	ψ(.)	γ(DL1)	ε(DL1)	*p*(A)
		4	ψ(.)	γ(DL1+S)	ε(DL1)	*p*(DL2)

occupied sites surrounding the site increased. In year 2, detection probability increased with the increased area and clumpiness of sand. In year 3, detection probability decreased as the area and fractal dimension of shinnery oak increased. Years 1 through 3 all had an additive seasonal effect, but the sessions did not have consistent detection probabilities across the years. Finally, in year 4, detection probability decreased with increased area and clumpiness of sand, which is the opposite trend from year 2. On the disturbed site, in year

1, detection probability increased slightly as the mean patch areas of the sand and road-well pad increased. Detection probability in years 2 and 3 increased as the percentage of occupied surrounding sub-grids increased. Detection probability in year 4 increased as the fractal dimensions of sand and oak increased.

Use

For the microhabitat models, in the undisturbed site, probability of use for years 1 and 4 increased as the mean slope increased and the mean substrate compaction decreased. In years 2 and 3, probability of use increased as the percent covers of shinnery oak and litter decreased. On the disturbed site, probability of use for years 2 and 4 increased as the percent cover of sand increased and the percent covers of shinnery oak and litter decreased. Probability of use for year 2 increased as the mean slope increased and the mean compaction decreased. Finally, probability of use in year 3 was constant ($\psi = 0.07 \pm 0.06$).

For the landscape models, for both sites, model results for the probability of use for all years showed that the landscape variables measured generally did not predict better than the constant use model (Table 4). Overall, on the disturbed site, years 2 and 4 had slightly higher probabilities of use than years 1 and 3. On the undisturbed site, the probability of use increased slowly each year in years 1 through 3 then declined slightly in year 4. On the undisturbed site, year 3 had an increase in probability of use as the area and clumpiness of sand increased; in year 4, probability of use decreased as the area and fractal dimension of oak patches increased.

Settlement and Vacancy

For the microhabitat models, probability of settlement at both sites had no consistent predictor variables (Table 4). In the undisturbed site, in year 1, probability of

settlement was constant ($\gamma = 0.22 \pm 0.08$). Year 2 probability of settlement varied across the trapping sessions. Year 3 probability of settlement increased as the mean slope increased and the mean substrate compaction decreased. Year 4 probability of settlement increased as the percent of occupied surrounding sites increased. On the disturbed site, year 1 probability of settlement was constant ($\gamma = 0.09 \pm 0.04$) and year 2 was inestimable. Probability of settlement in year 3 increased as the percent cover of sand increased and the percent covers of shinnery oak and litter decreased. Finally, in year 4, probability of settlement increased as the mean slope increased and mean substrate compaction decreased; however, it was only estimable in the middle and final trapping sessions.
For the microhabitat models, probability of vacancy was inestimable for years 1 and 3 on the undisturbed site and years 1, 3, and 4 on the disturbed site. On the undisturbed site, in year 2, probability of vacancy decreased as percent cover of shinnery oak and litter decreased, but was only estimable early and mid- season. In year 4, probability of vacancy increased as mean slope decreased and mean substrate compaction increased. On the disturbed site, in year 2, probability of vacancy increased as mean substrate compaction increased.

For the landscape models, settlement probabilities on the undisturbed site were consistently best predicted by models that included the autocovariate (percent occupied surrounding sub-grids; Table 4). For all four years, the probability of settlement increased as the percent of occupied surrounding sites increased. The probability of settlement in year 1 also had an additive effect of session, limiting estimates to the June-July and July-July transition periods. In year 2, probability of settlement also decreased as the area and clumpiness of sand patches increased. On the disturbed site, for years 1 and 3 the

probability of settlement decreased as the patch areas of sand and road- well pad increased, but in year 4, the probability of settlement increased as the patch areas of sand and road-well pad increased. In year 4, we also see an additive effect of session: early June and early August are the only sessions in which probability of settlement is estimable. Finally, for year 2, probability of settlement was constant ($\gamma = 0.16 \pm 0.07$).

For the landscape models at both sites, probability of vacancy was inestimable for year 1. On the undisturbed site, in years 2 and 3, probability of vacancy increased as the area and fractal dimension of shinnery oak patches increased. In year 3, we also saw an additive effect of the autocovariate where the probability of vacancy increased as the percentage of occupied surrounding sites increased, an unexpected result. Finally, in year 4, probability of vacancy was constant ($\varepsilon = 0.09 \pm 0.03$). On the disturbed site, in year 2, probability of vacancy was constant ($\varepsilon = 0.06 \pm 0.02$), while for years 3 and 4, the probability of vacancy increased as the patch areas of sand and road- well pad increased.

For the landscape models, we saw variations in the net differences between probability of settlement and probability of vacancy in years 2 through 4 (when both parameters are estimable; Table 4). On the undisturbed site, probability of settlement was equal to or higher than probability of vacancy in year 2 (Fig. 5D). This changed in years 3 and 4; in year 3 probability of settlement was equal to or lower than the probability of vacancy, a trend that strengthened in year 4 (Fig. 5E-F). On the disturbed site, again we saw very little consistent patterns in the variations in the net differences between probability of settlement and probability of vacancy in years 2 through 4 (when both parameters are estimable; Table 4). In year 2, probabilities of settlement and vacancy were constant resulting in a consistently high probability of settlement across the site (Fig. 5A).

In year 3, there was a split where some areas had fairly high probabilities of settlement, while others had high probabilities of vacancy (Fig. 5B). In year 4, there were again fairly high probabilities of settlement across the whole site (Fig. 5C). In both years 3 and 4, probability of vacancy increased as the patch areas of sand and road- well pad increased, but because probability of settlement for these two years had opposite relationships to the patch areas of sand and road- well pad, we saw different patterns in probabilities of settlement and vacancy across the site.

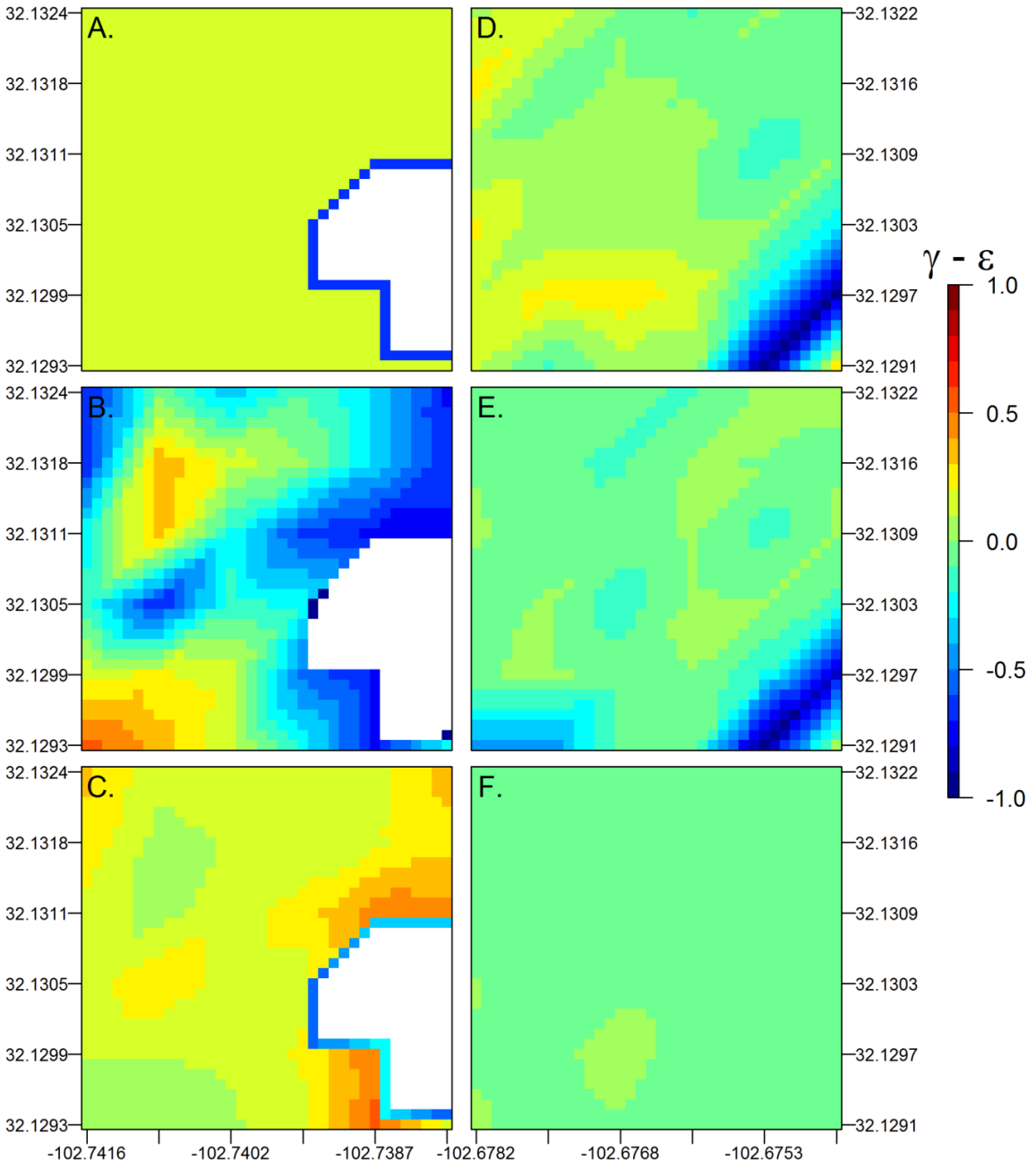

Figure 5 The difference between predicted probability of settlement (γ) and predicted probability of vacancy (ε) from the model averaged values from the top models from the landscape analyses, for each sub-grid. If settlement was greater than vacancy, values were positive; if settlement was less than vacancy, values were negative. A – C were the disturbed site for years 2-4 respectively. D – F were the undisturbed site for years 2 – 4, respectively. Probability of vacancy was inestimable for year 1 at both sites, so those estimates were not included. Values have been linearly interpolated across the site.

Discussion

Our results demonstrate that patterns of microhabitat and landscape context influence use, settlement, and vacancy in complex ways; microhabitat selection does not simply scale up to determine landscape-scale patterns of occupancy. As such, our study fills a knowledge gap in how movements of individuals are linked to larger scale patterns of species' distributions. Our study focused on settlement and vacancy patterns in a heterogeneous landscape occupied by a habitat specialist that depends on a specific landform, specifically shinnery oak dune blowouts. Our models gave important insights into how microhabitat use was linked to larger scale settlement and vacancy of areas in a continuous landscape.

Our prediction that microhabitat use should scale up to reflect the landscape patterns was only partly supported. The overarching pattern in our results was that microhabitat variables better predicted the probability of use, while landscape-scale variables better predicted probabilities of settlement and vacancy. Microhabitat variables important at small scales did not necessarily determine use of large-scale features (e.g. selection for high percent cover of sand at the microhabitat scale did not scale up to selection of large sand patches at the landscape scale). Conversely, it appears that for patterns of settlement and vacancy, *S. arenicolus* were selecting at larger scales for features that were not so apparent at the microhabitat scale. Each of these scales may be important for maintaining different population processes (Wiens et al. 1993). For example, at the microhabitat level, use is important because it determines day-to-day factors for individual survival: food availability, thermoregulation sites, and shelter from predators (Wiens et al. 1993). In the larger landscape context, settlement and vacancy is important because it

reflects larger scale population connectivity activities such as mate searching, nest-site selection, juvenile dispersal (Ryberg et al. 2013), and movements between sub-populations (Blevins and With 2011). Our study allows us to better understand some of the patterns of use, settlement, and vacancy by *S. arenicolus* and their relationship to specific landscape features at different scales.

Previous studies have identified that even within the dune ecosystem, *S. arenicolus* selected microhabitat sites based on specific variables (Fitzgerald et al. 1997, Hibbitts et al. 2013) and a hierarchy of habitat selection was described for this system (Fitzgerald and Painter 2009). In this study, steep slopes, loose sand, and shinnery oak cover seemed to be good predictors of fine scale variation in probability of use at the microhabitat scale. Additionally, on the disturbed site, *S. arenicolus* selected for areas with more sand and less shinnery oak cover. Previous studies converge on the importance of features of dune blowouts as strong predictors of microhabitat selection by *S. arenicolus*. Hibbitts et al. (2013) also showed *S. arenicolus* preferred steeper slopes and less compact soils in fragmented and unfragmented areas. Our results were similar in identifying these features as being important to *S. arenicolus* at the microhabitat scale.

It was not unsurprising that we observed complex temporal dynamics in habitat use. The shinnery oak dune ecosystem is a dynamic landscape, maintained by complex feedbacks between wind, sand, and vegetation (Ryberg et al. 2015). On the undisturbed site there was a cyclical pattern of use during this study (Fig. 6E-H). . In year 1, the probability of use of sub-grids by *S. arenicolus* was restricted to areas with larger, more extensive blowouts on the west side of the site, compared to very low probability of use on the east side of the site, where the blowouts were smaller and the landscape was

transitioning to flatter mesquite grasslands (Fig. 6B,E). In years 2 and 3, probability of use was better predicted by the percent cover of shinnery oak with a corresponding spread in the population to the east side of the undisturbed site (Fig. 6F-G). Finally, in year 4, the population was mostly using the largest dune areas on the west side of the site again, characterized by high mean slope and low mean substrate compaction (Fig. 6H). Habitat use associations can change over time, expanding in "good" years and becoming more restrictive in "bad" years (Sergio and Newton 2003, Hurme et al. 2008). Sergio and Newton (2003) found that *Milvus migrans* (black kite) occupied more low quality territories when population densities were higher, while high quality territories were preferred in all years. Additionally, Hurme et al. (2008) showed *Pteromys volans* (Siberian flying squirrels) had patches that were constantly occupied, while also having intermittently occupied patches that were of lesser quality but important for maintaining networks of habitat. Thus, we suggest the patterns of use by *S. arenicolus* on the undisturbed site could correspond to more constrained landscape use during non-optimal years.

In the disturbed site, we also quantified a dynamic response by lizards to the microhabitat features, but no consistent patterns of changing use over time. Instead, there were two areas of very high use in the north and southwestern parts of the site in years 1, 2, and 4 (Fig. 7E-F, H). Hibbitts et al. (2017) showed that even small caliche road tracks act as a barrier for *S. arenicolus*, which may partially explain why there were two core areas of habitat used on the disturbed site to the north and south of the road. Temporal dynamics may be especially important for local populations at the edges of a species' range, which

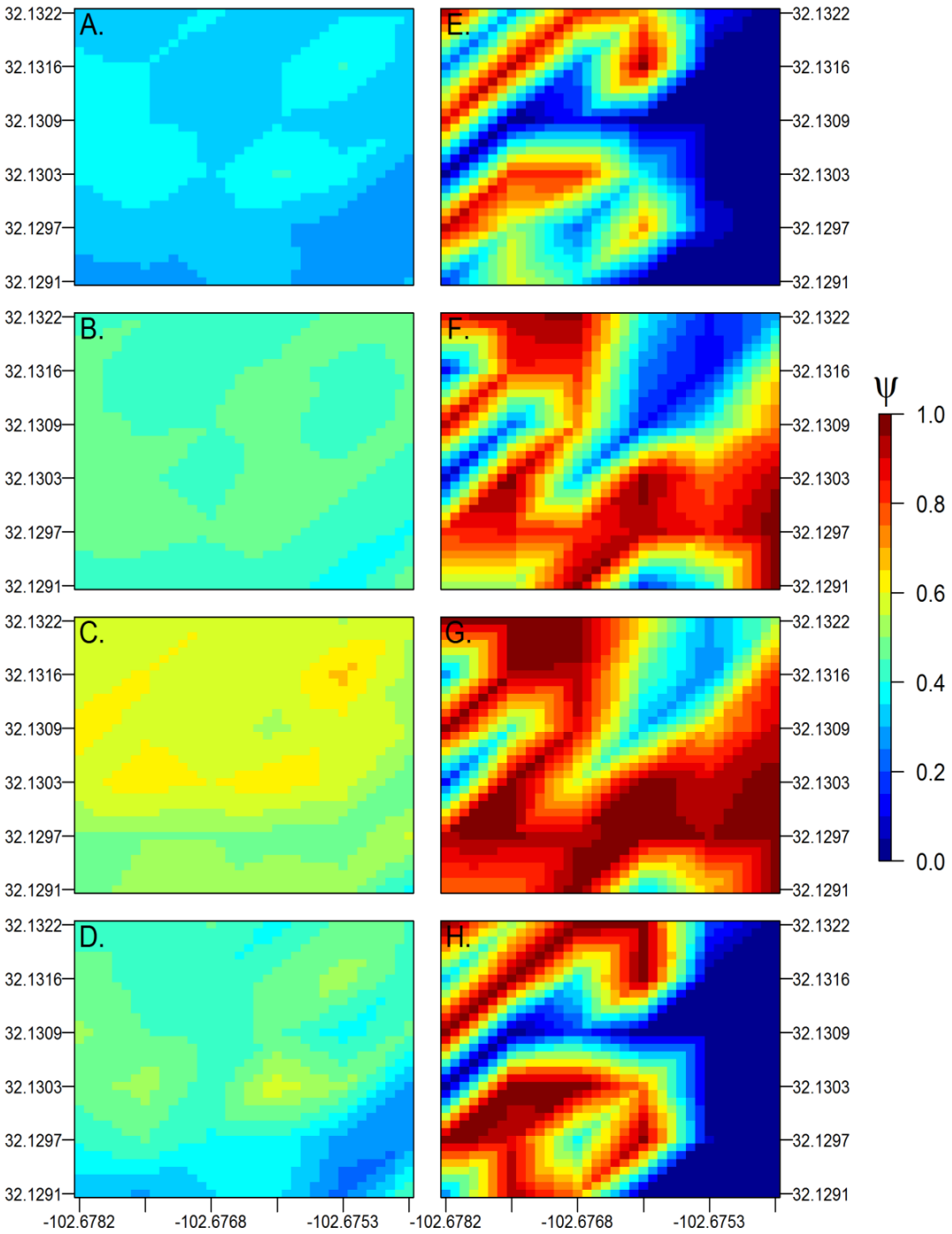

Figure 6 Predicted probability of use (ψ) on the undisturbed site. A – D are the model averaged results from the top models (constant, UL1, and UL2) in the landscape analysis for each sub-grid, for years 1-4 respectively. E – H are the model averaged results from the top model each year in the microhabitat analysis: (E) year 1 – ψ increased as mean slope increased, (F) year 2 – ψ increased as mean percent cover of shinnery oak increased, (C) year 3 – ψ increased as mean percent cover of shinnery oak increased, and (D) year 4 – ψ increased as mean slope increased. Values have been linearly interpolated across the site.

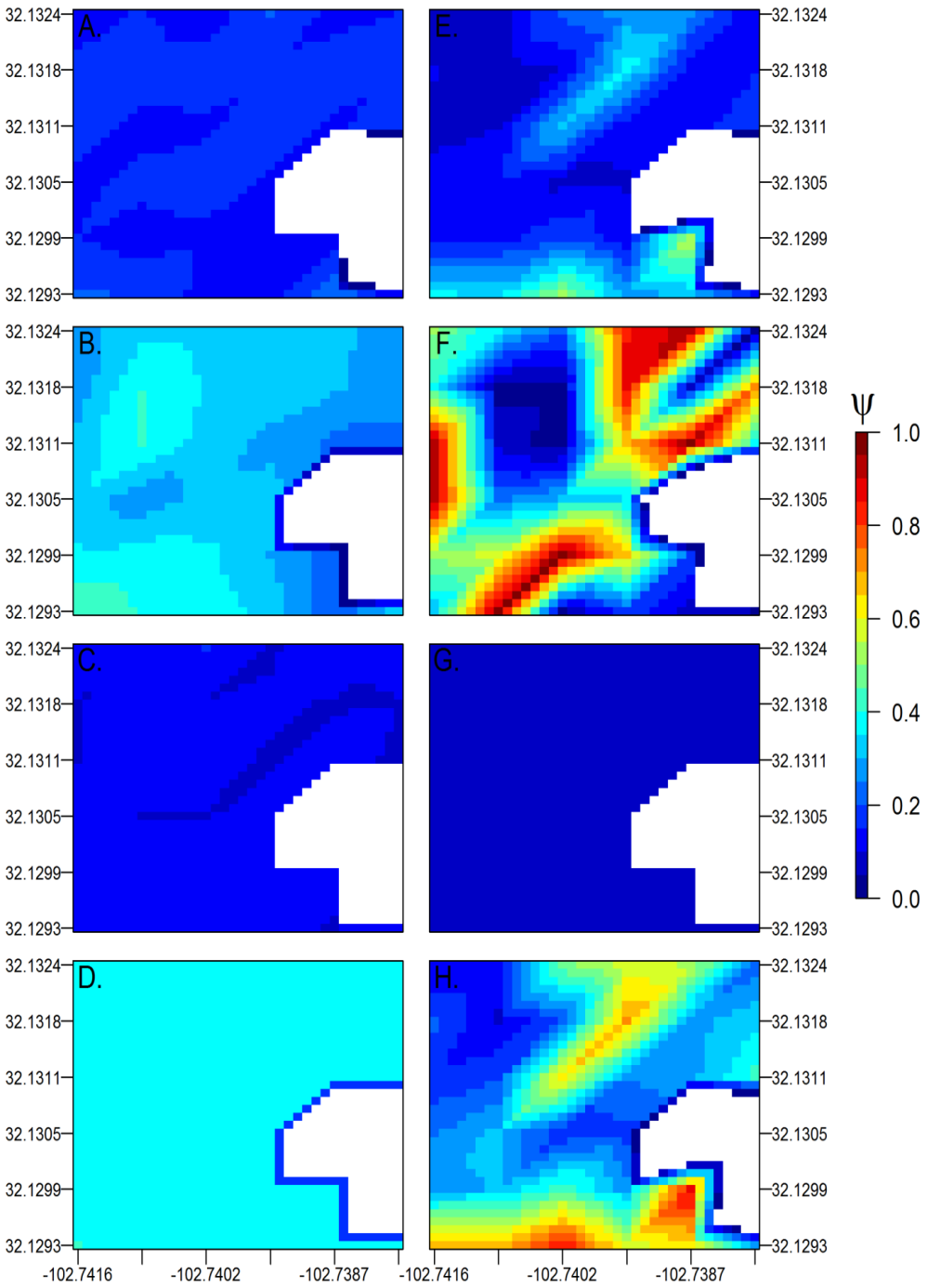

Figure 7 Predicted probability of use (ψ) on the disturbed site. A – D are the model averaged results from the top models (constant, DL1, and DL2) in the landscape analysis for each sub-grid, in years 1-4 respectively. E – H are the model averaged results from the top model each year in the microhabitat analysis: (E) year 1 – ψ increased as mean percent cover of sand increased, (F) year 2 – ψ increased as mean slope increased, (G) year 3 – ψ = 0.07 ± 0.06, and (H) year 4 – ψ increased as mean percent cover of sand increased. Values have been linearly interpolated across the site.

may fluctuate in response to local environmental changes (González-Megías et al. 2005, Yackulic et al. 2015). In our study, even though the two populations were only 5 km apart, the populations responded differently over time, and in different ways. In 2015, the final year of the study, there were heavy rain events early in the breeding season, resulting in lower captures and delayed emergence, breeding, and hatching of *S. arenicolus* on the undisturbed site (D. Walkup pers. obs.). However, on the disturbed site, we had double to triple the amount of captures than in the previous 3 years. Interestingly, even though there were almost twice as many captures in the final year on the disturbed site, we did not see a corresponding expansion in use; even though captures were much higher, the number of sub-grids with captures was about the same (Table 2). Similar patterns were observed in a different dune system. In coastal dunes in Argentina, a coastal dune-dwelling lizard species (*Liolaemus gracilis*) more than doubled its population density, while available habitat was reduced by 50% (Vega et al. 2000). In fragmented areas, *S. arenicolus* populations experienced severe disruptions in demographic structure, most likely due to extremely low abundance and increased demographic stochasticity, which ultimately led to local extirpations (Walkup et al. 2017). It is possible that *S. arenicolus* populations at the disturbed site may be showing some initial signs of the disrupted demography exhibited by populations in other areas, responding to the disturbances in and around this site.

The landscape models typically predicted the probability of settlement and vacancy parameters better than the microhabitat models, which were typically unable to estimate these parameters. This may reflect a hierarchical scaling of use; landscape variables were the initial determinants of colonization and extinction for some species, such as *Ammodramus henslowii* (Henslow's Sparrows), which first selected for large areas of

grasslands when settling in the spring (Herse et al. 2017). Landscape configuration was tightly linked to *S. arenicolus* neighborhood dynamics and population vital rates (Ryberg et al. 2013). Large lizard neighborhoods had relatively high levels of dispersal and were associated with specific features of the dune blowout landform. The sensitivity of vital rates was tightly linked to blowout shape (Ryberg et al. 2015). Interestingly, the only models for which the autocovariate was consistently and highly predictive were for probability of settlement in the undisturbed landscape-scale models. For this, the presence of *S. arenicolus* in surrounding sub-grids alone better predicted probability of settlement dynamics than did any of the landscape covariates. This may indicate that the population in this area was a source for *S. arenicolus*, sending out enough individuals that any effect of the landscape on the population was swamped out.

We also identified interesting temporal dynamics in the predictors of settlement and vacancy, both within the breeding season and between years. No single variable or suite of variables, at the microhabitat or landscape scale, consistently predicted vacancy and settlement. During the breeding season, settlement was typically higher both earlier in May when mating occurs and late in the season when hatchlings emerge. Settlement was lowest in early spring and during the hottest part of the breeding season. Notably, the predicted probabilities of settlement were consistently higher in the disturbed site in years 2 – 4 compared to the undisturbed site, yet still had lower naïve estimates of occupied sub-grids. So while the association with the sand and road- well pad patches indicated that *S. arenicolus* should be able to move more across the disturbed site, we did not observe those movements in *S. arenicolus'* use of the different sub-grids over the course of this study. This may be due to inconsistent reactions to different landscape features. For example, in

year 3, settlement was positively associated with the area of sand and caliche surfaces, but negatively associated in year 4. This changing association with the same covariate over those two years may be because it included a correlation between habitat (sand patches) and barriers to movement (road- well pad patches; Hibbitts et al. 2017, Young et al. 2018). Summarizing, our models offered insights into determinants of settlement of this species that were due to multiple features associated with disturbed and undisturbed landscapes, and interactions with the species' breeding phenology.

The configuration of landscape features, in particular the arrangement of shinnery dune blowouts, appear to be critically important for the maintenance of populations of *S. arenicolus*. The overarching conclusion from this study is that use, settlement, and vacancy in *S. arenicolus* populations were dynamic, and no single variable consistently predicted these dynamics. Our study informs linkages in how habitat selection made by individuals at two different scales results in variation in the spatio-temporal structure of the populations and informs the persistence of those populations within a continuous landscape. Habitat use changed across scales and over time in response to varying environmental conditions. This finding carries important conservation implications for this system and for habitat specialist species in general.

The importance of landscape scale features in settlement and vacancy dynamics in the Mescalero-Monahans Sandhills ecosystem indicated that for populations to maintain connectivity landscape-scale areas of shinnery oak dunelands must remain somewhat intact even if microhabitat patches can be identified at small scales. For example, our results showed how lack of detection of the target species in one area during one year does not necessarily mean that it may not be present over the long term. The distribution of

individuals in landscapes over time affects population dynamics and persistence of species, especially for habitat specialists (Ye et al. 2013a, b). Because of the close ties of the population dynamics of *S. arenicolus* to the configuration of shinnery oak dunes (Ryberg et al. 2013, 2015), fragmentation of contiguous areas of dunelands will make the species' range more patchy and with more potential barriers to dispersal. This study and previous work demonstrated *S. arenicolus* is unlikely to persist in disjunct habitat over time and also highlights why temporal variability in landscape use should be a consideration when developing conservation strategies for habitat specialists.

CHAPTER IV

OCCUPANCY AND DETECTION OF AN ENDEMIC HABITAT SPECIALIST, THE DUNES SAGEBRUSH LIZARD (*Sceloporus arenicolus*)

Synopsis

We estimated occupancy and extinction probabilities for the Dunes Sagebrush Lizard *Sceloporus arenicolus* for part of its range in Texas, to increase our understanding of the distribution of this species and to evaluate the likelihood of occurrence map that identifies areas according to Very High, High, Low, and Very Low categories. This map, developed using expert opinion, has been vital in establishing conservation policies for the species under the Texas Conservation Plan. From May to August 2014–2016, 100 16-ha sites were surveyed by crews of four observers who searched each quadrant of the sites for all lizards. Lizards were identified to species and tabulated, and GPS locations were recorded for *S. arenicolus*. Over 336 surveys, 33 *S. arenicolus* were detected during 17 surveys at nine sites in areas classified as Very High likelihood of occurrence. Occupancy probability for *S. arenicolus* in the Very High likelihood of occurrence areas was 0.32 ± 0.09 (SE), with a detection probability of 0.52 ± 0.12. Local extinction probabilities were low at 0.12 ± 0.18, with the colonization probability fixed at zero. *S. arenicolus* were detected in the 54% of surveys that occurred outside the currently recognized range. Thus, we are confident in the described range boundaries of *S. arenicolus*. The consistent predictability of occurrence of *S. arenicolus* in Very High likelihood of occurrence areas suggests recovery and conservation actions in areas that have the highest likelihood of occupancy should have highest priority.

Introduction

In recent research on squamates, the importance of estimating population parameters corrected by detection probabilities has been increasingly appreciated (Refsnider et al. 2011, Durso and Seigel 2015). Squamates have experienced population declines as a result of many causes, including habitat loss and degradation (agriculture, natural resource use, and urban development), pressure from invasive species, and resource harvesting (Gibbons et al. 2000, Böhm et al. 2013, Fitzgerald et al. 2018). Although population declines may be pervasive, they are also hard to detect, because reptile population abundances can vary widely over time from natural causes (Fitzgerald 1994, Mazerolle et al. 2007, Hibbitts et al. 2009). Temporal variation in the abundance or occurrence of reptile populations is notoriously stochastic, and presumed to be associated with fluctuating environmental conditions (e.g., drought), variable resources (Dunham 1981), and many other factors. Determining whether a decline is part of natural population fluctuations or driven by human activities poses a challenge for species conservation (Gibbons et al. 2000). Indeed, without baseline data and repeated monitoring to estimate detection probabilities, occupancy, and population parameters, population declines can go undetected until it may be too late (Tuberville et al. 2000, Winne et al. 2007, Hibbitts et al. 2009).

Occupancy modeling accounts for imperfect detectability when documenting the presence and absence of species (MacKenzie et al. 2002, 2003). By including detection probability as a parameter, these models address some biases in parameter estimation that occur under the assumption of perfect detection (MacKenzie et al. 2002, Gu and Swihart 2004). This assumption has been shown to be especially problematic for cryptic species

with secretive natural histories (Mazerolle et al. 2007). For lizards in particular, occupancy modeling has been used with great success to evaluate the effects of different habitat management practices on populations. For example, Blevins and With (2011) found Collared Lizards (*Crotaphytus collaris*) had higher occupancy in watersheds that were burned frequently, compared to those that were grazed or not burned. Occupancy modeling has also been used to guide management protocols for species such as the Christmas Island Blue-tailed Skink (*Cryptoblepharus egeriae,* Smith et al. 2012) and the Flat-tailed Horned Lizard (*Phrynosoma mccallii*, Leavitt et al. 2015). Occupancy modeling coupled with population abundance estimates has also proven useful in describing the establishment and dispersal of species, as in the case of the St. Croix Ground Lizard (*Ameiva polops*) that was translocated to Buck Island National Monument, US Virgin Islands (Fitzgerald et al. 2015, Angeli et al. 2018). Aside from these cases, occupancy and detection probabilities have not been reported for most lizard species of conservation concern. For example, while the geographic range and distribution of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*) has been well established (Laurencio and Fitzgerald 2010, Fitzgerald et al., 1997, 2011), estimates of occupancy and detection have not been previously determined.

Sceloporus arenicolus is a habitat specialist, endemic to the Mescalero-Monahans Sandhills ecosystem of west Texas and southeast New Mexico. It prefers large contiguous areas of shinnery oak dunes, and selects large, deep blowouts with steep sides (Fitzgerald and Painter 2009, Smolensky and Fitzgerald 2011, Hibbitts et al. 2013). Throughout the lizard's range, its presence is associated with areas where sand is composed of relatively high proportions of medium or coarse grains (Ryberg et al. 2012, 2015). Research on population dynamics and dispersal patterns revealed that *S. arenicolus* populations

exhibited source-sink dynamics across contiguous expanses of dunes, and the vital rates of *S. arenicolus* populations were directly linked to the configuration of dune blowouts in the landscape (Ryberg et al. 2013, Ryberg et al. 2015).

Sceloporus arenicolus is affected by large-scale and persistent conservation challenges across its range. The species' range overlies the Permian Basin, the world's second largest oil field, where approximately 14% of the United States' crude oil production occurs (Ewing et al., 2014). Extensive development of well-pad and road networks has led to fragmentation of shinnery oak dunes, negatively impacting *S. arenicolus* populations (Leavitt and Fitzgerald 2013, Walkup et al. 2017). In highly fragmented areas, the lizard community becomes disassembled, changing from a predictably structured community to one that is randomly structured (Leavitt and Fitzgerald 2013). The habitat specialist *S. arenicolus* disappears first, likely due to disruption of population structure (Walkup et al. 2017). *Sceloporus arenicolus* exhibits road avoidance behaviors toward even small, rarely traveled roads (Hibbitts et al. 2017), so the network of the road infrastructure appears to disrupt the movement dynamics across the landscape. With the extensive threats to *S. arenicolus* populations and habitat in Texas and the impetus from its proposed listing under the Endangered Species Act (US Fish and Wildlife Service 2010), the Texas Conservation Plan (TCP; Texas Comptroller of Public Accounts 2012) was put into place in 2012. The TCP is a conservation agreement with assurances that relies on voluntary participation built on a partnership among private landowners, industry, and state and federal agencies. The aim of the TCP is to incentivize participants to avoid habitat conversion for *S. arenicolus* in Texas, thereby minimizing the perceived risks of federal listing of *S. arenicolus*.

A key component of the TCP is a map of the range of *S. arenicolus* in Texas designating areas in four categories of likelihood of occurrence from Very High to Very Low (Fig. 8). This map was initially developed by Hibbitts and presented in Fitzgerald et al. (2011) to indicate the likelihood that *S. arenicolus* would be detected by surveys in the mapped categories. Shinnery oak dunes were delineated using aerial photography. All the areas contain what appears to be some suitable habitat for *S. arenicolus*. The four categories were created "based on known presence in an area, its connectivity to other areas, and on-the-ground assessment of habitat condition" (Fitzgerald et al. 2011, pg. 6). Areas classified as Very High or High likelihood of occurrence had known *S. arenicolus* records and shinnery dunes with large open blowouts. High likelihood of occurrence areas had fewer *S. arenicolus* records (i.e. less than half the surveys found *S. arenicolus*; T. Hibbitts, pers. comm.) and smaller contiguous areas of shinnery dunes than Very High areas. Areas classified as Low or Very Low likelihood of occurrence were areas where the *S. arenicolus* has not been found, and which contain more disjunct habitat patches separated by unsuitable areas. There is one confirmed locality in Crane County from 1970, but the species has not been detected in Crane Co. since.

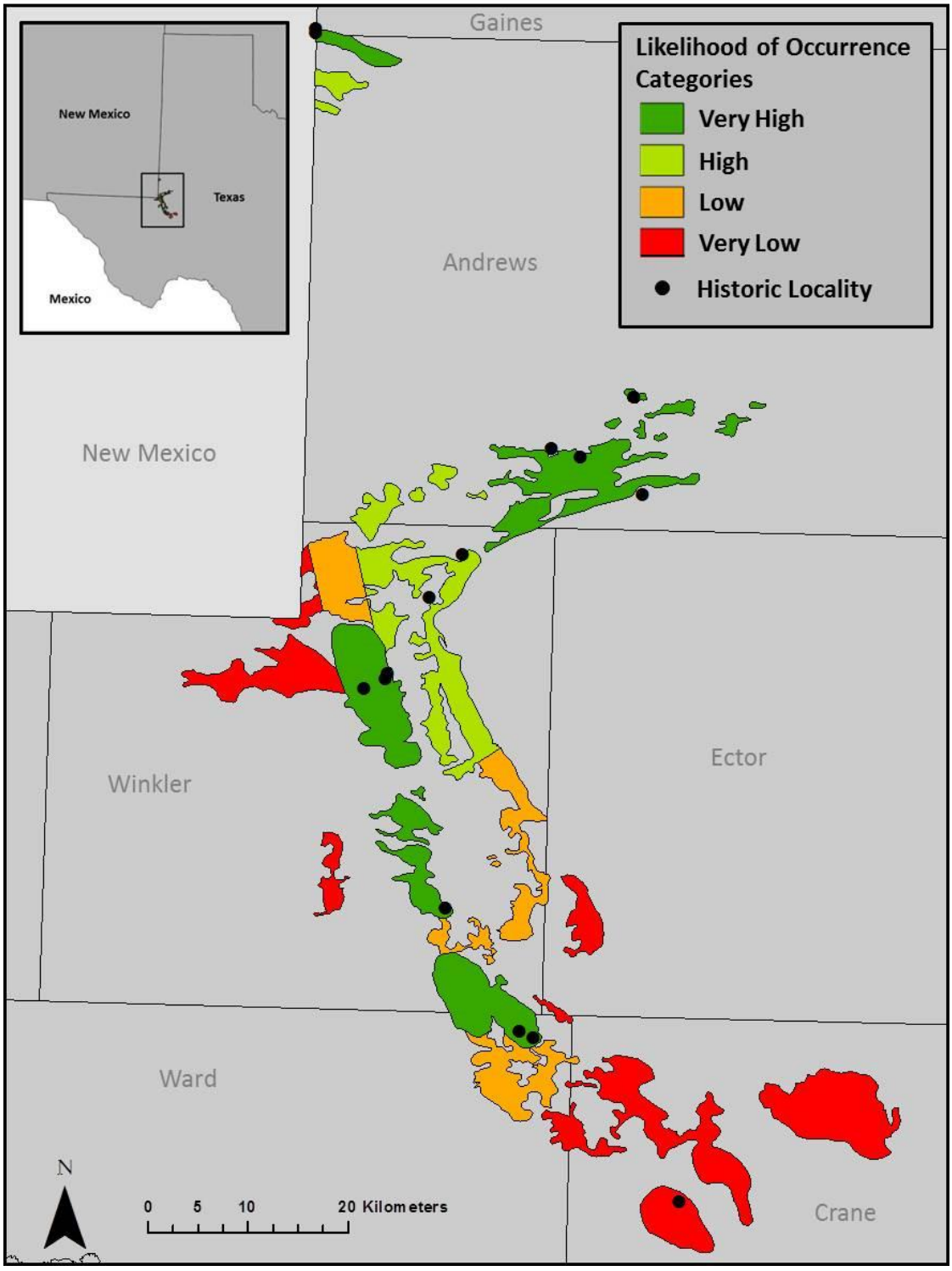

Figure 8 Map showing the currently recognized range of the Dunes Sagebrush Lizard in Texas with historical localities 1958–2010 (more recent records cannot be shown due to landowner confidentiality agreements). Colored areas denote the Likelihood of Occurrence categories for the Dunes Sagebrush Lizard used in implementing the Texas Conservation Plan.

This map was later incorporated into the TCP to guide management of the species in Texas and acts as a foundation for recovery values (Texas Comptroller of Public Accounts 2012). However, because the areas were derived through a qualitative process, the TCP leaders and stakeholders called for continued annual surveys to estimate occupancy of the species in Texas. The results from occupancy surveys would be used to monitor the persistence of *S. arenicolus* populations over time.

Our goal in this study was to create an occupancy model for *S. arenicolus* to increase our understanding of the pattern of presence and absence of the species. We also estimated the local extinction and colonization probabilities for *S. arenicolus* populations, to help understand how metapopulation dynamics may affect the distribution of this species. We provide the first estimates of detection probabilities related to the current survey protocols for this species. Finally, we used the occupancy model results to lend quantitative insights into the previously established areas of likelihood of occurrence.

Materials and Methods

We generated 16-ha square survey sites over the range of *S. arenicolus* in Texas and a subset of those generated sites were randomly selected to be surveyed. Most of this species' habitat in Texas is on private land, so our survey sites were limited to areas we had permission to access. In total, we selected 100 sites for surveys in four of the six counties with historical records of *S. arenicolus* (Andrews Co., n = 50 sites; Crane Co., n = 20 sites; Ward Co., n = 13 sites; Winkler Co., n = 17 sites) and which contain the majority of *S. arenicolus* habitat in Texas (Fig. 8). Sites were concentrated in areas of Very High likelihood of occurrence (n = 33) and areas outside of suitable habitat (n = 54), with fewer surveys in the other categories of occurrence (Low, n = 5; Very Low, n = 8) (Fig. 8). We

did not have any sites in the High category because we did not have access to properties in these areas. Areas considered to be outside of suitable habitat were close to the current known range (located from 0.3 to 3.6 km from the nearest range boundary) and were surveyed to more rigorously test for presence and absence around the known range.

We also surveyed areas considered to be outside of suitable habitat that were within 0.3 to 3.6 km from the nearest range boundary. Some of these areas did contain shinnery oak dunes, but not all of them. These were surveyed to more rigorously understand boundaries of the species' range in Texas.

Teams of qualified observers surveyed each site multiples times from 2014 to 2016. We targeted the months of May through August, which represented the months of peak lizard activity. During each survey, four observers (five observers participated in three surveys) divided the survey site into quadrants and one observer walked their quadrant searching for lizards for approximately 30 minutes. Surveys continued until the whole quadrant had been searched and did not stop when *S. arenicolus* was found. Surveys took place between 0830 and 1300h, corresponding to the morning activity period of *S. arenicolus*. One observer per quadrant reduced the possibility of duplicate observations of the same lizard and lessened chances that a lizard would be disturbed before it was detected. All lizards were identified to species and recorded. Locations where *S. arenicolus* were recorded with a Global Positioning System (GPS) unit (standard user precision only).

Using multi-season occupancy models, we estimated occupancy (ψ), detection probability (p), colonization probability (γ) and local extinction probability (ε) for the sites in the Very High likelihood of occurrence areas (the only area in which we had both detection/non-detection data; MacKenzie et al. 2003). We designed eight *a priori* models

to assess annual variation in the colonization, local extinction, and detection probabilities. Then, because estimates of colonization were so low in those 8 models, we added four more models where colonization probability was fixed at 0 (assuming that no sites were colonized during the course of this study). Survey data were aggregated into two sessions each year, from May to late June and late June to early August. As not all sites were surveyed each session, missing surveys were coded as ".", which resulted in large confidence intervals around some of the parameter estimates. Models were ranked via Akaike's Information Criterion corrected for small sample size (AIC_c), where the effective sample size was the number of sites included in the analysis (n = 33), and the "best" models were determined based on $\Delta AIC_c < 2.0$ (Burnham and Anderson 2002). All models were fit using program PRESENCE (Hines 2006). While the effectiveness of goodness-of-fit tests for multi-season models is debated, we used a parametric bootstrap (n = 5000) with a χ^2 fit statistic to test goodness-of-fit the most complex model (i.e. subglobal model), where $P > 0.05$ indicated a good fit (Burnham and Anderson 2002, MacKenzie and Bailey 2004), using the *parboot* function in the "unmarked" package (Fiske and Chandler 2011) in R (R Core Team 2017).

Results

During May 2014–August 2016, we conducted 339 Dunes Sagebrush Lizard surveys at 100 sites over most of the species' range in Texas (Table 2). A mean number of 3.39 surveys (range, 2–5 surveys) were conducted per site. We had 33 detections of *S. arenicolus* during 17 surveys at nine sites over the three years, and all of these were in the Very High likelihood of occurrence category. In contrast, *S. arenicolus* was not detected in 322 surveys at 91 sites. We detected *S. arenicolus* on every visit (n = 4 surveys) at only

one site in Andrews Co. *Sceloporus arenicolus* were detected in 3 out of 4 surveys at each of 2 sites in Andrews Co, and 2 out of 3 surveys at a third site in Winkler Co. At the remaining five sites (three in Andrews Co., one in Winkler Co., one in Ward Co.), we detected *S. arenicolus* only once despite conducting 2-4 surveys at each site. The time to first sighting of the target species varied among surveys. We detected *S. arenicolus* within 60 person-minutes (e.g. four observers searching for 15 minutes) during nine of the 17 positive surveys, and between 60 and 120 person-minutes in six of these 17 surveys. In the remaining two positive surveys, *S. arenicolus* were detected after 128 and 144 person-minutes. The average time to detection was 65 ± (SD) 39 person-minutes (range, 5–144 person-minutes, n = 17). The duration of surveys where *S. arenicolus* was found ranged from 120 to 163 person-minutes (mean search time = 142 ± (SD) 12 person-minutes, n =17), while surveys where *S. arenicolus* was not detected ranged from 100 to 170 person-minutes (mean search time = 128 ± (SD) 11 person-minutes, n = 322). In the surveys <120 min, the four observers had thoroughly covered all potential habitat in the survey area.

No *S. arenicolus* were detected during the 183 surveys on sites that fell outside the known range of *S. arenicolus* in Texas (Fig. 4). Additionally, no *S. arenicolus* were detected in 37 surveys at five sites in Low and eight sites in Very Low likelihood of occurrence areas. Because there were no detections in these areas, we elected not to estimate occupancy probabilities for the Low, and Very Low likelihood of occurrence areas, as well as any survey sites that fell outside these areas; non-detection and non-occupancy are confounded in areas with no detections.

Table 5 Number of surveys conducted for *Sceloporus arenicolus* in Texas 2014–2016 by likelihood of occurrence class. Surveys conducted outside the predicted areas of occurrence are also included.

Likelihood of Occurrence	2014	2015	2016	Total	Proportion	Dunes Sagebrush Lizards Detected
Very High	42	45	32	119	35.1%	33
High	0	0	0	0	0.0%	N/A
Low	0	9	4	13	3.8%	0
Very Low	0	16	8	24	7.1%	0
Outside	58	75	50	183	54.0%	0
Total				339	100.0%	33

Because we only had detections in the Very High likelihood of occurrence areas, our multi-season occupancy model was limited to the 33 sites in the Very High likelihood of occurrence model. Based on the parametric bootstrap, the subglobal model fit the data well (P = 0.42). The top model was the null model with colonization probability fixed at 0 (Table 3). Occupancy probability from the top model was 0.32 ± (SE) 0.09 (95% CI = 0.13–0.50), detection probability was 0.52 ± (SE) 0.12 (95% CI = 0.28–0.76), and local extinction probability was 0.12 ± (SE) 0.19 (95% CI = 0.00–0.49).

Table 6 Top candidate models of the multiple-season occupancy analysis for the Very High likelihood of occurrence areas in the Texas range of *Sceloporus arenicolus* during 2014–2016. Abbreviations are as follows: number of parameters (K), Akaike's Information Criterion corrected for small sample sizes (AIC_c), yearly estimates (yr), and constant (.).

Model	K	AIC_c	ΔAIC_c	AIC_c Weights	Cumulative Weights
ψ_i γ=0 ε(.) p(.)	3	87.80	0.00	0.57	0.57
ψ_i γ=0 ε(yr) p(.)	4	90.26	2.46	0.17	0.74
ψ_i γ(.) ε(.) p(.)	4	90.39	2.59	0.16	0.90
ψ_i γ=0 ε(.) p(yr)	5	93.02	5.22	0.04	0.94
ψ_i γ(.) ε(yr) p(.)	5	93.05	5.25	0.04	0.98
ψ_i γ(.) ε(.) p(yr)	6	96.03	8.23	0.01	0.99
ψ_i γ=0 ε(yr) p(yr)	6	96.03	8.23	0.01	1.00

Discussion

This study provided the first estimates of occupancy and colonization-extinction dynamics for *S. arenicolus* in a portion of its range. Our top occupancy model, with detection-corrected estimates of occupancy probabilities, suggests that *S. arenicolus* occupied approximately a third of the sites we surveyed in the Very High likelihood of occurrence areas. This low occupancy probability in the Very High likelihood of occurrence areas could be a result of the resolution of the Likelihood of Occurrence map, source-sink population dynamics of *S. arenicolus*, or simply a characteristic common to many endemic habitat specialists.

Because the Likelihood of Occurrence map polygons covered broad areas, there is some heterogeneity in the habitat represented within these areas. Thus, we would expect that not every site in the Very High likelihood of occurrence categories would be occupied based on the heterogeneous landscape alone. *Sceloporus arenicolus* is known to prefer relatively large dunes with correspondingly large blowouts; areas with large dunes and blowouts are more topographically complex with steep slopes, loose sand, and thermally favorable microsites (Fitzgerald et al. 1997, Fitzgerald and Painter 2009, Hibbitts et al. 2013). While these large dune complexes are a dominant feature in the Very High likelihood of occurrence areas, they are not the only landscape type in those areas. Our 16-ha sites were randomly chosen, because our goal was to estimate occupancy within the Very High likelihood of occurrence area. For this study, we chose to avoid bias in occupancy estimates by using targeted surveys aimed at the largest dune complexes (i.e., areas of interconnected dunes with blowouts) (MacKenzie et al. 2006). Thus, our sites often contained elements of the landscape not preferred by *S. arenicolus* (e.g., mesquite

flats, caliche roads, and oil and gas well pads), which could contribute to lower occupancy in Very High likelihood of occurrence areas.

However, map resolution and landscape heterogeneity cannot completely account for low occupancy. Many of the sites where *S. arenicolus* were not detected contained large expanses of shinnery oak dunes with blowouts. Previous research on the population dynamics and dispersal of *S. arenicolus* revealed that populations exhibited source-sink dynamics across contiguous occupied habitat (Ryberg et al. 2013), and that vital rates of *S. arenicolus* populations were linked to the configuration of dune blowouts in the landscape (Ryberg et al. 2015). Thus, it is also plausible the relatively low occupancy probabilities observed were in part due to metapopulation dynamics in this species playing out across the landscape. Due to constraints on dispersal in *S. arenicolus*, we suggest that localized extinctions and slow to nonexistent colonization would also result in low occupancy probabilities even among sites with large, deep contiguous blowouts that are preferred by *S. arenicolus*.

Low occupancy probabilities may be characteristic of many narrowly endemic habitat specialists. Habitat specialists typically exhibit patchy distributions, which reflect the distribution of habitat patches. Habitat specialists may also not occur in all available patches. As such, when habitat for these species is considered at larger landscape scales; the species may not be present in all available habitats (With and Crist 1995, Holt 1997). The occupancy probabilities that we calculated for *S. arenicolus* fell well within the range of occupancy probabilities seen in other studies of narrowly endemic lizard habitat specialists. We find that other habitat specialists tend to have lower occupancy probabilities than do lizards considered to be habitat generalists. This trend is reflected

especially among lizards that specialize in sandy habitats, such as the Florida Sand Skink (*Plestiodon reynoldsi*; ψ = 0.36–0.45) or the Sand Lizard (*Lacerta agilis*) in England (Rizkalla et al 2015, and Sewell et al. 2012, respectively). Occupancy probabilities for the Sand Lizard throughout southeast England ranged from 0.14–0.32; these estimates were much lower than those for a more widespread habitat generalist, the Common Lizard (*Zootoca vivipera*; ψ = 0.76–0.81), from the same study (Sewell et al. 2012). Additionally, occupancy probabilities of the more generalist species, the Toad-headed Agama (*Phrynocephalus versicolor*) in Mongolia, exhibited an inverse relationship to rocky outcroppings, where occupancy probabilities increased from 0 to 0.95 as the proportion of rocky habitat decreased from 1 to 0 (Murdoch et al. 2013). However, more research is needed to better understand generalities in lizard occupancy that may be related to life history characteristics, like degree of habitat specialization.

Our estimates of local extinction probability were fairly low, with high variability around the mean (0.14 ± 0.18 SE). Colonization probabilities were incredibly low (0.008 ± 0.098 SE) for our third ranked model, thus we felt that holding them to zero, as in the top two models, in this analysis was justified and helped to reduce variation around the other parameters. Very low colonization rates were unsurprising, considering the patchy distribution of *S. arenicolus*. For example, *S. arenicolus* were collected from Crane County in 1970, but the species has not been found there since despite multiple surveys at and surrounding the historical locality (Laurencio et al. 2007, Fitzgerald et al. 2011, this study). Population genetic studies also lend some support to this idea. Chan et al. (2009) found that genetic structure within and among populations of *S. arenicolus* revealed a pattern of very low inter-population migration and recent reductions in some populations.

Given the large number of surveys outside of the likelihood of occurrence polygons, we are confident in concluding *S. arenicolus* likely does not occur outside the currently recognized range boundaries in Texas. The species' range is also clearly limited by extent of the shinnery dunes landform. Unfortunately, because we could not get access to habitat located on private lands, there were no surveys in the High likelihood of occurrence areas, and we were unable to estimate probability of occupancy in this category. Although the Very High and High likelihood of occurrence areas contain patches of shinnery oak dunes with large dunes and blowouts that *S. arenicolus* prefers, there were very few historical localities in the High category versus many in the Very High category, which led to the difference in categorization of these areas. Though we expect occupancy to be less in the High likelihood of occurrence areas compared to the Very High areas, it is also probable that *S. arenicolus* are present at some locations that have never been surveyed. Having more sites distributed among all the categories, and three or more surveys/site each season would strengthen future occupancy analyses conducted in this system (MacKenzie 2005).

Detection probability of *S. arenicolus* in the Very High likelihood of occurrence areas was fairly high (0.52 ± 0.12). Other approaches for estimating population parameters for *S. arenicolus* have yielded similar findings. Smolensky and Fitzgerald (2010) derived a detection probability of 0.489 ± 0.065 using double-observer visual surveys and distance sampling transects at sites in New Mexico that were known to be historically occupied. An intensive five-year pitfall trapping study at 27 historically occupied sites in New Mexico returned detection probabilities ranging from 0.50 to 0.85 during the breeding season (D. J. Leavitt et al., unpubl. data). Unfortunately, because non-occupancy and non-detection are

confounded, we were unable to estimate a detection probability for the rest of our survey sites where no *S. arenicolus* were detected. If *S. arenicolus* occur at sites in Low and Very Low likelihood of occurrence areas, it is likely they will be present in the largest areas of shinnery dunes and at relatively low abundances. To determine if *S. arenicolus* occur in these areas, we suggest directing effort towards surveys at more sites, with fewer surveys per site, as the best way to get estimates of detection and occupancy in those areas (MacKenzie and Royle 2005).

Variation in effectiveness of survey methodologies leads to variation in detection probabilities (Zylstra et al. 2010, Michael et al. 2012, Rodda et al. 2015). One source of this variation stems from availability bias, where lizards that are not active are unavailable to be detected. Availability bias violates the base assumption that all lizards on the transect line are available for detection (Buckland et al. 2001) and is a known problem in the use of distance sampling methodologies to estimate population densities for many species, including *S. arenicolus* (Smolensky and Fitzgerald 2010). Another important source of variation in detection probabilities of lizards is due to seasonal and daily activity patterns. Lizard activity patterns vary by day, season, and among years (e.g. Seddon et al. 2011, Gebauer et al. 2013, Lardner et al. 2015, Rizkalla et al. 2015). Previous research showed seasonal variation in detection of *S. arenicolus* with detection probabilities lowest in mid-summer (July), after the breeding season, but before emergence of juveniles (D. J. Leavitt et al., unpubl. data). Detections in our surveys took place during May, June, and July, indicating that within season variation in activity may not have had the same impact on active surveys as it does in pitfall trapping studies. To fully understand the influence of seasonal activity on lizard detection, a study using repeated surveys during the year at a

number of sites would be needed. However, in terms of conservation and management, it is clear that occupancy surveys yield the most useful information when conducted during the peak activity season.

In summary, our results suggest our survey method was fairly effective for finding *S. arenicolus* where suitable habitat for this narrowly distributed habitat specialist was present. Because of the species' requirement for shinnery oak dunes with interconnected blowouts and rugose (i.e., bumpy) topography, it was found entirely in the Very High likelihood of occurrence category. It is important that surveys be conducted in the High likelihood of occurrence areas because the species has historically been found in portions of these areas and habitat condition is similar to that in the Very High areas in some places. To add more certainty to our findings, additional surveys are needed in the Low and Very Low likelihood of occurrence areas to estimate occupancy and detectability of *S. arenicolus* in these areas. Although we cannot conclude the species is absent from these areas, it is fairly certain that *S. arenicolus* are absent or very uncommon throughout the Low and Very Low likelihood of occurrence areas, especially given the long term accumulation of surveys from independent studies (Laurencio et al. 2007, Fitzgerald et al. 2011, this study). Because of the dynamics of colonization and local extinction that occur over very long time scales, it is critical to recognize that the current state of occupancy may not necessarily reflect the future state at a site. Periodic monitoring of the occurrence of the dune sagebrush lizard throughout its range will be necessary to document extinction and colonization of suitable habitat in the future. This is the first report of occupancy and detection for *S. arenicolus* using standardized surveys and can serve to inform future

monitoring aimed at understanding how land use may impact the distribution of the species.

CHAPTER V

CONCLUSIONS

I studied the distribution, habitat use, and response to fragmentation of a habitat specialist lizard, *Sceloporus arenicolus* (dunes sagebrush lizard). This species was an ideal subject for this research because *S. arenicolus* populations have been shown to be highly dependent on the landscape configuration (Ryberg et al. 2013), which is altered by fragmentation. There is a well-understood hierarchical scaling of habitat use in this system, from regional scale down to a very local scale (Fitzgerald 1997, 2011, Smolensky and Fitzgerald, 2011; Hibbitts et al. 2013), that my research complements. My research has shown: 1) fragmentation of the habitat impacted the population structure of *S. arenicolus*, resulting in the eventual extirpation of sub-populations over time, 2) habitat use expanded and contracted over time as *S. arenicolus* selected for different microhabitat characteristics, while the settlement and vacancy of individuals over the landscape was strongly tied to landscape features, and 3) finally, at the range wide scale, even within a patchy landscape, *S. arenicolus* was patchily distributed, and it took multiple surveys over time to confirm that *S. arenicolus* was not present at a site.

Understanding the characteristics of species that are impacted most by fragmentation can help mitigate the effects of fragmentation on these species (Andrén et al., 1997). Finding broad life history characteristics of species that allow us to predict their persistence in fragmented landscapes is a longstanding goal (e.g. Henle et al. 2004, Rytwinski and Fahrig, 2012). Habitat specialists in particular, due to their narrow niche breadth, are thought to be susceptible to changes in the habitat resulting from landscape

fragmentation (Swihart et al. 2003; Henle et al., 2004; Devictor et al., 2008). Results from Chapter II supported theoretical predictions of Henle et al. (2004), that the specialist species was much more susceptible to landscape fragmentation than the generalist species. I showed the mechanism by which the habitat specialist, *S. arenicolus,* populations decline in fragmented areas is through the disruption of the population structures. This presumably leads to eventual extirpation, as when capture rates of *S. arenicolus* declined to zero in fragmented habitat (Chapter II). In comparison, the generalist species, *Uta stansburiana* (common side-blotched lizard) and *Aspidoscelis marmorata* (marbled whiptail) appeared to thrive in the fragmented sites, with much higher capture rates compared to the unfragmented sites. However, other factors can also affect species responses to fragmentation, as another generalist species, *Holbrookia maculata* (common lesser earless lizard) exhibited a pattern of decline similar to *S. arenicolus*, although the decline was not as pronounced. This research enhanced the picture of how fragmentation may cause demographic disruption and decline of some species while having little effect on others.

Patch characteristics have been shown to mitigate the effects of fragmentation for some species (Jellinek et al. 2004, Devictor et al. 2008). For habitat specialists, Ye et al. (2013a, b) showed that spatial variation in within-patch quality controlled population abundance and moderated the effects of habitat fragmentation on their populations. Thus, understanding how species use and move through continuous habitat can have important implications for their responses to fragmentation (Gray et al. 2005). Studies across vertebrates have shown that selection for habitat use and movements occurs at multiple scales and that ignoring variation and interactions among microhabitat or landscape-scale habitat characteristics could result in misleading conclusions (Cornell and Donovan 2010,

Frey et al. 2012). In Chapter III, I showed that *S. arenicolus* was using habitat at two different scales. Microhabitat variables were better predictors of habitat use than were the landscape variables, showing that day to day population maintenance activities occurred at localized scales. For the settlement and vacancy, I found that the landscape covariates better predicted these two parameters than did the microhabitat, showing that for movements that influence population connectivity, *S. arenicolus* is moving through sites based on the broader habitat composition and configuration. Thus, Chapter III highlights why temporal variability in landscape use should be a consideration when developing conservation strategies for habitat specialists.

My dissertation has broad implications for conservation of *S. arenicolus*. First it suggests that in an already patchy habitat, *S. arenicolus* maintains a low probability of occupancy, even in habitat considered to have a very high likelihood of occurrence (Chapter IV). Because of *S. arenicolus*' requirement for shinnery oak dunes with interconnected blowouts and rugose (i.e., bumpy) topography, it was found entirely in the Very High likelihood of occurrence category in the surveys for Chapter IV. *Sceloporus arenicolus* were also likely absent or very uncommon throughout the Low and Very Low likelihood of occurrence areas, especially given the long term accumulation of surveys from independent studies in addition to this chapter (Laurencio et al. 2007; Fitzgerald et al. 2011). It is imperative that surveys be conducted in the High likelihood of occurrence areas because the species has historically been found in portions of these areas and habitat condition is similar to that in the Very High areas in some places. Although, I provided some baseline estimates of occupancy and detection for *S. arenicolus*, these likely already represent a shifted baseline, given the long history of development in the Mescalero

Monahans Sandhills ecosystem. However, understanding the current state of *S. arenicolus* populations across the range, using standardized surveys, can inform future monitoring aimed at understanding how land use may impact the distribution of the species. Periodic monitoring of the occurrence of *S. arenicolus* throughout its range will be necessary to document extinction and colonization of suitable habitat in the future.

Prior research in the Mescalero Monhans Sandhills ecosystem has shown that, even in continuous landscapes, *S. arenicolus* neighborhoods consist of local sources and sinks that were tied to the configuration of the landscape (Ryberg et al. 2013). In Chapter III, the composition and configuration of the landscape was important for movements that resulted in settlement and vacancy across a continuous landscape. Because *S. arenicolus* movements in continuous habitat are dependent on the landscape configuration, it implies that if the landscape configuration is disrupted, the movements are likely to be disrupted as well. Thus, as more of the continuous landscape is fragmented, then more of the movements are disrupted, eventually disrupting the overall population connectivity. This suggests that the populations should end up in smaller, more isolated sub-populations, leading to demographic disruption and eventual extirpation as demonstrated in Chapter II. Understanding these patterns at small scales, like these individual sites (Chapters II and III) help us to start to understand large scale distributions of *S. arenicolus* (Chapter IV) and focus on meaningful conservation strategies.

Here, I suggest that conservation studies should be focused on maintaining the landform of the Mescalero-Monhans Sandhills ecosystem. Fragmentation of the landscape is a persistent challenge in the Mescalero-Monahans Sandhills ecosystem and modifications of the landscape for installing well-pads and connecting roads require

changes to the structure of the habitat that may have long term impacts on how the landform itself persists (Ryberg et al. 2015). The Permian Basin is one of the largest oil fields in the United States and accounts for 14% of this country's oil production (Ewing et al. 2014). With advances in hydraulic fracturing and the new growth of sand mining for local use in hydraulic fracturing, production of oil and gas in the Permian Basin is likely to increase a lot in the next few years (Austin-American Statesman, 2018). Because *S. arenicolus* is a dune specialist, it is important that the development is done carefully, with an eye towards keeping broad landscape structure in place and allowing for diffusion of the species throughout the landscape to maintain population connectivity across this patchy landform.

In summary, I have shown how habitat fragmentation impacts *S. arenicolus* populations. Chapter II lent insight into the linkages between disturbance of landscape features and the consequences for populations. Once a population was small enough to have a disrupted demographic structure, the population was susceptible to decline and eventual local extirpation from normal fluctuations in the environment. Because *S. arenicolus* make choices about habitat use at the microhabitat scale, their daily activities (e.g. food, shelter, avoiding predation) may be less directly impacted by habitat fragmentation. But, because their movements (i.e. settlement and vacancy) are tied to landscape configuration and composition, these may be more directly impacted by fragmentation. The specific requirements of *S. arenicolus* for specific characteristics of dune blowouts within the Mescalero Monahans Sandhills ecosystem may be met in fragmented areas, but the landscape characteristics that allow for movement among habitat are likely disrupted by fragmentation as barriers to movement and some habitat loss occur.

With the low probability of occupancy exhibited by *S. arenicolus* across their range in Texas, it is important to maintain available habitat to allow for regular population functioning and connectivity.

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APPENDIX A

Model results from the dynamic occupancy modeling.

Table A1 Top models (delta AIC ≤ 2) results for the landscape models for the undisturbed site. Model covariates are: (.) = constant model; A = autocorrelation; S = Session (time effect); UL1 = large, aggregated sand patches to small, disaggregated sand patches gradient; UL2 = large, complex shinnery oak patches to small, simple shinnery oak patches gradient.

	Model				nPars	AIC	ΔAIC	AICwt	cumltvWt
Year 1	ψ(.)	γ(A+S)	ε(UL1)	p(A+S)	14	681.79	0.00	0.11	0.11
	ψ(UL2)	γ(A+S)	ε(UL1)	p(A+S)	15	682.44	0.66	0.08	0.18
	ψ(UL1)	γ(A+S)	ε(UL1)	p(A+S)	15	682.93	1.14	0.06	0.24
	ψ(.)	γ(A)	ε(UL1)	p(A+S)	11	683.45	1.66	0.05	0.29
	ψ(.)	γ(S)	ε(UL1)	p(A+S)	13	683.56	1.77	0.04	0.33
	ψ(UL1)	γ(A)	ε(UL1)	p(A+S)	12	683.93	2.15	0.04	0.37
Year 2	ψ(.)	γ(UL1+A)	ε(UL2)	p(UL1+S)	16	1117.40	0.00	0.20	0.20
	ψ(UL2)	γ(UL1+A)	ε(UL2)	p(UL1+S)	17	1118.68	1.29	0.10	0.30
	ψ(.)	γ(A+S)	ε(UL2)	p(UL1+S)	22	1119.20	1.80	0.08	0.38
	ψ(.)	γ(UL1+A)	ε(UL2+A)	p(UL1+S)	17	1119.30	1.90	0.08	0.46
	ψ(UL1)	γ(UL1+A)	ε(UL2)	p(UL1+S)	17	1119.39	1.99	0.07	0.53
	ψ(.)	γ(A)	ε(UL2)	p(UL1+S)	15	1120.49	3.09	0.04	0.58
Year 3	ψ(UL1)	γ(A)	ε(UL2+A)	p(UL2+S)	17	974.67	0.00	0.13	0.13
	ψ(.)	γ(A)	ε(UL2+A)	p(UL2+S)	16	974.88	0.21	0.12	0.24
	ψ(UL1)	γ(UL2+A)	ε(UL2+A)	p(UL2+S)	18	975.45	0.79	0.09	0.33
	ψ(.)	γ(UL2+A)	ε(UL2+A)	p(UL2+S)	17	975.70	1.03	0.08	0.41
	ψ(UL1)	γ(UL1+A)	ε(UL2+A)	p(UL2+S)	18	976.08	1.41	0.06	0.47
	ψ(.)	γ(UL1+A)	ε(UL2+A)	p(UL2+S)	17	976.33	1.67	0.06	0.53
	ψ(UL1)	γ(A)	ε(UL2)	p(UL2+S)	16	976.66	2.00	0.05	0.57
	ψ(UL2)	γ(A)	ε(UL2+A)	p(UL2+S)	17	976.69	2.02	0.05	0.62
Year 4	ψ(UL2)	γ(A)	ε(.)	p(UL1)	7	902.51	0.00	0.04	0.04
	ψ(UL2)	γ(UL1+A)	ε(.)	p(UL1)	8	902.89	0.38	0.03	0.07
	ψ(UL2)	γ(A)	ε(UL2)	p(UL1)	8	903.02	0.51	0.03	0.11
	ψ(UL2)	γ(UL1+A)	ε(UL2)	p(UL1)	9	903.43	0.91	0.03	0.13
	ψ(UL2)	γ(A)	ε(.)	p(UL1+A)	8	903.59	1.07	0.02	0.16
	ψ(UL1)	γ(A)	ε(.)	p(UL1)	7	903.88	1.37	0.02	0.18
	ψ(.)	γ(A)	ε(.)	p(UL1)	6	903.93	1.42	0.02	0.20
	ψ(UL2)	γ(UL1+A)	ε(.)	p(UL1+A)	9	903.97	1.46	0.02	0.22
	ψ(UL1)	γ(A)	ε(UL2)	p(UL1)	8	903.98	1.46	0.02	0.24
	ψ(.)	γ(A)	ε(UL2)	p(UL1)	7	904.09	1.58	0.02	0.25
	ψ(UL2)	γ(A)	ε(UL2)	p(UL1+A)	9	904.09	1.58	0.02	0.27
	ψ(UL2)	γ(A)	ε(A)	p(UL1)	8	904.15	1.63	0.02	0.29
	ψ(UL2)	γ(A)	ε(UL1)	p(UL1)	8	904.20	1.68	0.02	0.31
	ψ(.)	γ(UL1+A)	ε(.)	p(UL1)	7	904.25	1.74	0.02	0.32
	ψ(UL2)	γ(A)	ε(UL2+A)	p(UL1)	9	904.37	1.86	0.02	0.34

Table A1 Continued

	Model			nPars	AIC	ΔAIC	AICwt	cumltvWt
Year 4	ψ(UL1)	γ(UL1+A) ε(.)	p(UL1)	8	904.43	1.92	0.02	0.36
	ψ(.)	γ(UL1+A) ε(UL2)	p(UL1)	8	904.45	1.94	0.02	0.37
	ψ(UL2)	γ(UL2+A) ε(.)	p(UL1)	8	904.48	1.97	0.02	0.39
	ψ(UL2)	γ(UL1+A) ε(UL2)	p(UL1+A)	10	904.50	1.99	0.02	0.40
	ψ(UL1)	γ(UL1+A) ε(UL2)	p(UL1)	9	904.58	2.07	0.01	0.42

Table A2 Top models (delta AIC ≤ 2) results for the landscape models for the disturbed site. Model covariates are: (.) = constant model; A = autocorrelation; DL1 = large shinnery oak patches to large sand and road- well pad patches gradient; DL2 = highly aggregated sand patches to complex sand and shinnery oak patches gradient; S = Session (time effect).

	Model				nPars	AIC	ΔAIC	AICwt	cumltvWt
Year 1	ψ(.)	γ(DL1)	ε(DL2+S)	p(DL1)	10	256.77	0.00	0.04	0.04
	ψ(.)	γ(DL1)	ε(DL2+S)	p(DL2)	10	257.54	0.77	0.03	0.07
	ψ(.)	γ(DL1)	ε(DL2)	p(DL1)	7	257.55	0.78	0.03	0.10
	ψ(.)	γ(.)	ε(DL2+S)	p(DL2)	9	257.81	1.04	0.03	0.13
	ψ(.)	γ(DL2)	ε(DL2+S)	p(DL1)	10	257.96	1.19	0.02	0.15
	ψ(.)	γ(.)	ε(DL2+S)	p(DL1)	9	258.08	1.31	0.02	0.17
	ψ(.)	γ(DL2)	ε(DL2+S)	p(DL2)	10	258.32	1.55	0.02	0.19
	ψ(.)	γ(DL1)	ε(DL2+S)	p(DL2+A)	11	258.41	1.64	0.02	0.21
	ψ(.)	γ(DL1)	ε(DL2)	p(DL2)	7	258.41	1.64	0.02	0.23
	ψ(DL2)	γ(DL1)	ε(DL2+S)	p(DL1)	11	258.47	1.70	0.02	0.25
	ψ(.)	γ(A)	ε(DL2+S)	p(DL1)	10	258.49	1.72	0.02	0.27
	ψ(.)	γ(DL2)	ε(DL2+S)	p(DL2+A)	11	258.50	1.73	0.02	0.29
	ψ(.)	γ(DL1+A)	ε(DL2+S)	p(DL1)	11	258.58	1.81	0.02	0.30
	ψ(DL2)	γ(.)	ε(DL2+S)	p(DL1)	10	258.63	1.86	0.02	0.32
	ψ(.)	γ(.)	ε(DL2+S)	p(DL2+A)	10	258.74	1.97	0.02	0.34
	ψ(.)	γ(DL2)	ε(DL2)	p(DL1)	7	258.78	2.01	0.02	0.35
Year 2	ψ(.)	γ(.)	ε(.)	p(A)	5	402.90	0.00	0.04	0.04
	ψ(DL1)	γ(.)	ε(.)	p(A)	6	402.99	0.09	0.04	0.07
	ψ(.)	γ(DL1)	ε(.)	p(A)	6	403.87	0.98	0.02	0.09
	ψ(.)	γ(.)	ε(A)	p(A)	6	404.31	1.41	0.02	0.11
	ψ(DL1)	γ(.)	ε(A)	p(A)	7	404.34	1.44	0.02	0.13
	ψ(.)	γ(DL2)	ε(.)	p(A)	6	404.36	1.46	0.02	0.15
	ψ(DL1)	γ(DL2)	ε(.)	p(A)	7	404.40	1.50	0.02	0.17
	ψ(.)	γ(.)	ε(DL2)	p(A)	6	404.63	1.73	0.02	0.18
	ψ(DL1)	γ(.)	ε(DL2)	p(A)	7	404.64	1.74	0.02	0.20
	ψ(DL2)	γ(.)	ε(.)	p(A)	6	404.77	1.88	0.01	0.21
	ψ(DL1)	γ(.)	ε(.)	p(DL1+A)	7	404.78	1.88	0.01	0.23
	ψ(DL1)	γ(DL1)	ε(.)	p(A)	7	404.81	1.91	0.01	0.24
	ψ(.)	γ(.)	ε(DL1)	p(A)	6	404.86	1.96	0.01	0.25
	ψ(.)	γ(A)	ε(.)	p(A)	6	404.87	1.98	0.01	0.27
	ψ(.)	γ(.)	ε(.)	p(DL1+A)	6	404.90	2.00	0.01	0.28
	ψ(.)	γ(.)	ε(.)	p(DL2+A)	6	404.90	2.00	0.01	0.29
Year 3	ψ(.)	γ(DL1)	ε(DL1)	p(A)	7	404.35	0.00	0.06	0.06
	ψ(.)	γ(DL1)	ε(DL1+A)	p(A)	8	404.81	0.46	0.05	0.11
	ψ(.)	γ(.)	ε(DL1)	p(DL2+A)	7	404.94	0.59	0.05	0.16
	ψ(.)	γ(DL2)	ε(DL1)	p(DL2+A)	8	405.61	1.26	0.03	0.19
	ψ(DL1)	γ(DL1)	ε(DL1)	p(A)	8	406.10	1.75	0.03	0.22
	ψ(.)	γ(DL1+A)	ε(DL1)	p(A)	8	406.12	1.77	0.03	0.25
	ψ(DL2)	γ(DL1)	ε(DL1)	p(A)	8	406.17	1.82	0.03	0.27
	ψ(DL2)	γ(.)	ε(DL1)	p(DL2+A)	8	406.23	1.88	0.03	0.30
	ψ(.)	γ(A)	ε(DL1)	p(DL2+A)	8	406.32	1.97	0.02	0.32

Table A2 Continued

	Model				nPars	AIC	ΔAIC	AICwt	cumltvWt
Year 3	ψ(DL1)	γ(.)	ε(DL1)	p(DL2+A)	8	406.32	1.97	0.02	0.34
	ψ(.)	γ(.)	ε(DL1)	p(A)	6	406.47	2.12	0.02	0.37
Year 4	ψ(.)	γ(DL1+S)	ε(DL1)	p(DL2)	14	598.25	0.00	0.05	0.05
	ψ(.)	γ(DL1+S)	ε(A)	p(DL2)	14	598.67	0.42	0.04	0.09
	ψ(.)	γ(S)	ε(A)	p(DL2)	13	598.68	0.43	0.04	0.13
	ψ(.)	γ(S)	ε(.)	p(DL2)	12	598.83	0.58	0.04	0.17
	ψ(.)	γ(DL1+S)	ε(.)	p(DL2)	13	599.41	1.16	0.03	0.20
	ψ(.)	γ(DL1+S)	ε(DL1)	p(DL2+A)	15	599.63	1.38	0.03	0.22
	ψ(DL2)	γ(DL1+S)	ε(DL1)	p(DL2)	15	600.15	1.90	0.02	0.24
	ψ(DL1)	γ(DL1+S)	ε(DL1)	p(DL2)	15	600.23	1.98	0.02	0.26
	ψ(.)	γ(DL1+S)	ε(A)	p(DL2+A)	15	600.26	2.01	0.02	0.28

Table A3 Top models (delta AIC ≤ 2) results for the microhabitat models for the undisturbed site. Model covariates are: (.) = constant model; A = autocorrelation; S = Session (time effect); UM1 = high average slope to high average compaction gradient; UM2 = high to low percent cover of oak and litter gradient.

	Models				nPars	AIC	ΔAIC	AICwt	Cum.Wt
Year 1	ψ(UM1)	γ(.)	ε(UM2+A)	p(UM1+S)	11	627.97	0.00	0.30	0.30
	ψ(UM1)	γ(.)	ε(UM2+A)	p(UM1+S)	12	629.48	1.51	0.14	0.44
	ψ(UM1)	γ(A)	ε(UM2+A)	p(UM1+S)	13	630.14	2.17	0.10	0.54
Year 2	ψ(UM2)	γ(S)	ε(UM2+S)	p(UM1)	21	1051.53	0.00	0.16	0.16
	ψ(UM2)	γ(A+S)	ε(UM2+S)	p(UM1)	22	1051.80	0.26	0.14	0.29
	ψ(UM2)	γ(UM1+S)	ε(UM2+S)	p(UM1)	22	1052.23	0.70	0.11	0.40
	ψ(UM2)	γ(UM2+S)	ε(UM2+S)	p(UM1+S)	30	1052.87	1.33	0.08	0.48
	ψ(UM2)	γ(S)	ε(UM2+S)	p(UM1+A)	22	1053.43	1.89	0.06	0.54
	ψ(UM2)	γ(UM2+S)	ε(UM2+S)	p(UM1)	22	1053.52	1.99	0.06	0.60
	ψ(UM2)	γ(A+S)	ε(UM2+S)	p(UM1+A)	23	1053.79	2.26	0.05	0.65
Year 3	ψ(UM2)	γ(UM1)	ε(UM1)	p(UM1+S)	16	894.29	0.00	0.36	0.36
	ψ(UM2)	γ(UM1+A)	ε(UM1)	p(UM1+S)	17	896.27	1.99	0.13	0.49
	ψ(UM2)	γ(UM1)	ε(UM1+A)	p(UM1+S)	17	896.29	2.00	0.13	0.62
Year 4	ψ(UM1)	γ(A)	ε(UM1)	p(UM1)	8	860.66	0.00	0.10	0.10
	ψ(UM1)	γ(.)	ε(UM1)	p(UM1)	7	860.85	0.19	0.10	0.20
	ψ(UM1)	γ(.)	ε(UM1+A)	p(UM1)	8	861.12	0.46	0.08	0.28
	ψ(UM1)	γ(UM1)	ε(UM1)	p(UM1)	8	861.16	0.49	0.08	0.36
	ψ(UM1)	γ(A)	ε(UM1+A)	p(UM1)	9	861.49	0.83	0.07	0.43
	ψ(UM1)	γ(UM1)	ε(UM1+A)	p(UM1)	9	861.74	1.08	0.06	0.49
	ψ(UM1)	γ(UM1+A)	ε(UM1)	p(UM1)	9	862.14	1.47	0.05	0.54
	ψ(UM1)	γ(UM1)	ε(UM1)	p(UM1)	9	862.51	1.85	0.04	0.59
	ψ(UM1)	γ(UM2)	ε(UM1)	p(UM1)	8	862.64	1.98	0.04	0.62
	ψ(UM1)	γ(A)	ε(UM1)	p(UM1+A)	9	862.66	2.00	0.04	0.66

Table A4 Results for the Microhabitat Variables for the West Grid, with models having delta AIC ≤ 2. Model covariates are: (.) = constant model; A = autocorrelation; DM1 = high average slope to high average compaction gradient; DM2 = high oak and litter cover to high sand cover gradient; S = Session (time effect).

	Models				nPars	AIC	ΔAIC	AICwt	Cum.Wt
Year 1	ψ(DM2)	γ(.)	ε(DM2+S)	p(.)	9	257.99	0.00	0.06	0.06
	ψ(DM2)	γ(DM1)	ε(DM2+S)	p(.)	10	258.23	0.24	0.05	0.12
	ψ(DM2)	γ(.)	ε(DM2+S)	p(A)	10	259.12	1.13	0.03	0.15
	ψ(.)	γ(DM1)	ε(DM2+S)	p(.)	9	259.26	1.27	0.03	0.18
	ψ(.)	γ(.)	ε(DM2+S)	p(.)	8	259.36	1.37	0.03	0.22
	ψ(DM2)	γ(.)	ε(DM2+S)	p(DM2)	10	259.80	1.81	0.02	0.24
	ψ(DM2)	γ(DM1)	ε(DM2+S)	p(A)	11	259.81	1.82	0.02	0.27
	ψ(DM2)	γ(A)	ε(DM2+S)	p(.)	10	259.86	1.87	0.02	0.29
	ψ(DM2)	γ(DM2)	ε(DM2+S)	p(.)	10	259.91	1.92	0.02	0.31
	ψ(DM2)	γ(.)	ε(DM2+A)	p(.)	7	259.91	1.92	0.02	0.34
	ψ(DM2)	γ(DM1+A)	ε(DM2+S)	p(.)	11	260.02	2.03	0.02	0.36
Year 2	ψ(DM1)	γ(DM2+S)	ε(DM1+A)	p(DM1+A)	17	384.23	0.00	0.27	0.27
	ψ(DM1)	γ(DM2+S)	ε(DM1)	p(DM1+A)	16	384.60	0.37	0.22	0.49
	ψ(DM1)	γ(DM2)	ε(DM1)	p(DM1+A)	9	386.79	2.56	0.08	0.57
Year 3	ψ(.)	γ(DM2)	ε(A+S)	p(DM1)	14	406.69	0.00	0.13	0.13
	ψ(DM2)	γ(DM2)	ε(A+S)	p(DM1)	15	407.45	0.76	0.09	0.21
	ψ(.)	γ(DM2+A)	ε(A+S)	p(DM1)	15	407.55	0.86	0.08	0.30
	ψ(DM1)	γ(DM2)	ε(A+S)	p(DM1)	15	407.64	0.95	0.08	0.38
	ψ(.)	γ(DM1)	ε(A+S)	p(DM1)	14	408.66	1.97	0.05	0.42
	ψ(.)	γ(.)	ε(A+S)	p(DM1)	13	408.66	1.97	0.05	0.47
	ψ(DM2)	γ(DM2)	ε(A+S)	p(DM1+A)	16	408.81	2.12	0.04	0.52
Year 4	ψ(DM2)	γ(DM1+S)	ε(DM2+A)	p(DM2)	16	590.60	0.00	0.73	0.73
	ψ(DM2)	γ(DM1+S)	ε(A)	p(DM2)	15	596.67	6.07	0.04	0.76

Table A5 Landscape model averaged beta estimates of the top model for the undisturbed site. Model covariates are: (.) = constant model; A = autocorrelation; S = Session (time effect); UL1 = large, aggregated sand patches to small, disaggregated sand patches gradient; UL2 = large, complex shinnery oak patches to small, simple shinnery oak patches gradient.

	Parameter	Covariate	Beta	SE	95% LCL	95% UCL
Year 1	ψ	Intercept	-0.73	0.38	-1.47	0.02
		UL1	0.33	0.33	-0.31	0.97
		UL2	-0.43	0.44	-1.29	0.43
	γ	Intercept	-28.38	227.39	-474.05	417.3
		A	2.95	1.68	-0.34	6.24
		S – Jun	54.48	328.06	-588.50	697.47
		S – Jul1	55.84	328.07	-587.17	698.84
		S – Jul2	3.16	357.67	-697.86	704.17
	ε	Intercept	-63.04	97.26	-253.68	127.59
		UL1	41.89	58.71	-73.19	156.97
	p	Intercept	-0.07	0.30	-0.65	0.51
		A	-1.98	0.54	-3.04	-0.92
		S – Jun	-0.63	0.37	-1.36	0.01
		S – Jul1	-1.07	0.38	-1.83	-0.32
		S – Jul2	0.42	0.36	-0.29	1.12
		S – Aug	-0.44	0.34	-1.10	0.22
Year 2	ψ	Intercept	-0.22	0.39	-0.98	0.54
		UL1	-0.07	0.35	-0.75	0.62
		UL2	-0.28	0.35	-0.96	0.41
	γ	Intercept	-3.90	1.23	-6.31	-1.48
		A	4.16	1.77	0.69	7.62
		UL1	-0.66	0.38	-1.4	0.08
	ε	Intercept	-2.82	1.14	-5.05	-0.59
		UL2	2.13	1.3	-0.41	4.67
	p	Intercept	-0.42	0.28	-0.97	0.14
		UL1	0.37	0.08	0.21	0.53
		S – Apr2	0.21	0.37	-0.52	0.94
		S – May1	-0.15	0.36	-0.85	0.56
		S – May2	-0.25	0.37	-0.97	0.48
		S – Jun1	-0.68	0.38	-1.43	0.07
		S – Jun2	-0.18	0.36	-0.89	0.53
		S – Jul1	-0.70	0.39	-1.46	0.05
		S – Jul2	-1.23	0.4	-2.02	-0.45
		S – Aug	-0.66	0.38	-1.39	0.08
Year 3	ψ	Intercept	0.20	0.42	-0.63	1.03
		UL1	0.43	0.32	-0.19	1.05
		UL2	-0.20	0.64	-1.45	1.05
	γ	Intercept	-3.69	2.72	-9.02	1.63
		A	3.19	1.43	0.39	6.00

Table A5 Continued

	Parameter	Covariate	Beta	SE	95% LCL	95% UCL
Year 3	ε	Intercept	-2.57	1.23	-4.98	-0.17
		UL2	1.46	0.69	0.11	2.80
		A	3.68	2.02	-0.27	7.63
	p	Intercept	-1.14	0.27	-1.67	-0.62
		UL2	-0.38	0.18	-0.74	-0.02
		S – Apr2	-0.71	0.41	-1.52	0.09
		S – May1	0.87	0.36	0.17	1.58
		S – May2	1.13	0.37	0.41	1.85
		S – Jun1	0.55	0.36	-0.16	1.26
		S – Jun2	0.42	0.40	-0.36	1.19
		S – Jul1	0.04	0.40	-0.74	0.83
		S – Jul2	0.24	0.39	-0.52	1.00
		S – Aug	0.06	0.42	-0.77	0.89
Year 4	ψ	Intercept	-0.41	0.38	-1.16	0.34
		UL1	0.44	0.34	-0.24	1.12
		UL2	-0.76	0.53	-1.8	0.28
	γ	Intercept	-4.60	2.99	-10.46	1.26
		A	4.24	1.83	0.64	7.83
	ε	Intercept	-2.30	0.64	-3.57	-1.04
	p	Intercept	-0.58	0.17	-0.90	-0.25
		UL1	-0.32	0.08	-0.47	-0.16

Table A6 Landscape model averaged beta estimates of the top model for the disturbed site. Model covariates are: (.) = constant model; A = autocorrelation; DL1 = large shinnery oak patches to large sand and road- well pad patches gradient; DL2 = highly aggregated sand patches to complex sand and shinnery oak patches gradient; S = Session (time effect).

	Parameter	Covariate	Beta	SE	95% LCL	95% UCL
Year 1	ψ	Intercept	-1.74	0.70	-3.11	-0.38
		DL2	0.54	0.75	-0.93	2.00
	γ	Intercept	-2.82	26.13	-54.03	48.39
		DL1	-0.64	0.47	-1.56	0.27
	ε	Intercept	-12.69	28.31	-68.16	42.79
		DL2	34.92	77.91	-117.77	187.62
		S – Jun	-46.46	128.16	-297.65	204.74
		S – Jul1	4.71	29.35	-52.82	62.24
		S – Jul2	33.37	74.80	-113.24	179.99
	p	Intercept	-1.91	0.39	-2.68	-1.15
		DL1	0.08	0.10	-0.11	0.27
Year 2	ψ	Intercept	-0.82	0.51	-1.81	0.18
		DL1	-0.62	0.53	-1.66	0.41
		DL2	-0.18	0.42	-1.00	0.65
	γ	Intercept	-2.91	4.18	-11.1	5.29
	ε	Intercept	-1.57	0.60	-2.75	-0.39
	p	Intercept	-2.44	0.31	-3.04	-1.84
		A	3.23	1.02	1.24	5.23
Year 3	ψ	Intercept	-2.47	1.49	-5.39	0.45
		DL1	-0.42	0.96	-2.29	1.46
		DL2	-0.80	1.09	-2.93	1.33
	γ	Intercept	-2.67	2.19	-6.97	1.63
		DL1	-2.14	1.90	-5.87	1.59
	ε	Intercept	-14.99	47.55	-108.18	78.21
		DL1	-10.22	39.75	-88.12	67.69
	p	Intercept	-2.22	0.68	-3.55	-0.90
		A	2.47	1.91	-1.27	6.22
Year 4	ψ	Intercept	-0.47	0.38	-1.21	0.26
		DL1	-0.05	0.26	-0.56	0.45
		DL2	0.11	0.34	-0.56	0.78
	γ	Intercept	-10.00	31.44	-71.62	51.61
		DL1	0.75	0.52	-0.26	1.76
		S – Apr2	-0.94	84.27	-166.09	164.22
		S – May1	-1.07	67.10	-132.60	130.45
		S – May2	7.52	32.46	-56.10	71.13
		S – Jun1	-1.32	70.23	-138.97	136.32
		S – Jun2	-0.36	55.03	-108.22	107.50
		S – Jul1	-0.48	52.20	-102.80	101.83
		S – Jul2	9.81	32.45	-53.79	73.41

Table A6 Continued

	Parameter	Covariate	Beta	SE	95% LCL	95% UCL
Year 4	ε	Intercept	-1.82	0.78	-3.35	-0.30
		DL1	0.36	0.29	-0.20	0.93
	p	Intercept	-1.25	0.22	-1.69	-0.82
		DL2	0.39	0.11	0.18	0.60

Table A7 Microhabitat model averaged beta estimates of the top model for the undisturbed site. Model covariates are: (.) = constant model; A = autocorrelation; S = Session (time effect); UM1 = high average slope to high average compaction gradient; UM2 = high to low percent cover of oak and litter gradient; NE = not estimable.

	Parameter	Covariate	Beta	SE	95% LCL	95% UCL
Year 1	ψ	Intercept	-2.04	1.16	-4.30	0.23
		UM1	-10.77	4.63	-19.85	-1.69
	γ	Intercept	-3.61	64.13	-129.31	122.09
		Constant	-1.24	0.43	-2.08	-0.39
	ε	Intercept	NE	-	-	-
	p	Intercept	-2.09	0.35	-2.77	-1.41
		UM1	-4.20	0.67	-5.51	-2.88
Year 2	ψ	Intercept	0.93	0.85	-0.72	2.59
		UM2	11.39	5.54	0.53	22.26
	γ	Intercept	-1.01	1.61	-4.16	2.14
		S – Apr2	0.25	1.76	-3.21	3.7
		S – May1	-9.19	60.02	-126.82	108.44
		S – May2	-8.12	45.22	-96.75	80.51
		S – Jun1	-8.35	128.20	-259.63	242.92
		S – Jun2	-8.57	55.11	-116.58	99.44
		S – Jul1	0.23	1.62	-2.95	3.41
		S – Jul2	2.11	2.02	-1.85	6.07
	ε	Intercept	-4.3	36.91	-76.64	68.04
		UM2				
		S – Apr2	2.11	37.95	-72.28	76.49
		S – May1	-7.44	103.36	-210.02	195.14
		S – May2	-10.19	154.84	-313.66	293.29
		S – Jun1	-6.78	83.74	-170.90	157.34
		S – Jun2	3.52	36.97	-68.94	75.99
		S – Jul1	5.67	37.15	-67.14	78.48
		S – Jul2	-7.40	104.61	-212.44	194.64
	p	Intercept	-1.82	0.25	-2.31	-1.34
		UM1	-4.86	0.54	-5.91	-3.8
Year 3	ψ	Intercept	2.14	1.19	-0.20	4.48
		UM2	12.59	6.82	-0.78	25.97
	γ	Intercept	-1.98	11.59	-24.69	20.73
		UM1	-4.5	2.09	-8.6	-0.40
	ε	Intercept	NE	-	-	-
	p	Intercept	0.47	1.45	-2.38	3.32
		UM1	8.73	4.1	0.69	16.77

Table A7 Continued

	Parameter	Covariate	Beta	SE	95% LCL	95% UCL
Year 3	p	Intercept	-1.83	0.28	-2.39	-1.28
		UM1	-3.04	0.71	-4.43	-1.64
		S – Apr2	-0.60	0.42	-1.42	0.22
		S – May1	0.80	0.36	0.10	1.51
		S – May2	0.99	0.37	0.27	1.71
		S – Jun1	0.46	0.35	-0.23	1.15
		S – Jun2	0.17	0.38	-0.58	0.91
		S – Jul1	-0.18	0.39	-0.94	0.57
		S – Jul2	0.03	0.37	-0.69	0.76
		S – Aug	-0.23	0.38	-0.98	0.53
Year 4	ψ	Intercept	-2.05	1.51	-5.02	0.91
		UM1	-20.71	15.20	-50.51	9.09
	γ	Intercept	-2.95	2.50	-7.85	1.96
		A	2.50	2.07	-1.56	6.56
	ε	Intercept	0.47	1.45	-2.38	3.32
		UM1	8.73	4.1	0.69	16.77
	p	Intercept	-1.52	0.30	-2.11	-0.93
		UM1	-2.64	0.81	-4.23	-1.05

Table A8 Microhabitat model averaged beta estimates of the top model for the disturbed site. Model covariates are: (.) = constant model; A = autocorrelation; DM1 = high average slope to high average compaction gradient; DM2 = high oak and litter cover to high sand cover gradient; S = Session (time effect).

	Parameter	Covariate	Beta	SE	95% LCL	95% UCL
Year 1	ψ	Intercept	-1.70	0.83	-3.31	-0.08
		DM2	6.43	4.28	-1.97	14.83
	γ	Intercept	-3.12	59.79	-120.31	114.07
		DM1	-1.93	1.57	-5.00	1.14
	ε	Intercept	NE	-	-	-
	p	Intercept	-2.06	0.34	-2.72	-1.41
Year 2	ψ	Intercept	-0.46	0.64	-1.71	0.78
		DM1	-10.67	7.65	-25.66	4.32
	γ	Intercept	-85.20	94.14	-269.70	99.31
	ε	Intercept	0.46	2.16	-3.77	4.70
		A	-10.33	13.89	-37.56	16.90
		DM1	48.57	28.83	-7.92	105.07
	p	Intercept	-2.57	0.25	-3.06	-2.08
		A	4.36	0.96	2.47	6.24
		DM1	2.61	0.80	1.05	4.16
Year 3	ψ	Intercept	-2.61	1.02	-4.60	-0.62
	γ	Intercept	-2.46	14.38	-30.64	25.73
		DM2	3.43	1.54	0.41	6.45
	ε	Intercept	NE	-	-	-
	p	Intercept	-2.15	0.29	-2.70	-1.59
		DM1	-2.10	0.73	-3.54	-0.67
Year 4 *	ψ	Intercept	-0.56	0.43	-	-
		DM2	5.45	2.59	-	-
	γ	Intercept	-16.67	266.16	-	-
		DM1	-6.19	2.74	-	-
		S – Apr2	-2.47	568.58	-	-
		S – May1	-4.28	593.22	-	-
		S – May2	13.65	266.16	-	-
		S – Jun1	-2.50	572.51	-	-
		S – Jun2	-1.19	518.78	-	-
		S – Jul1	-0.43	464.51	-	-
		S – Jul2	15.46	266.16	-	-
	ε	Intercept	NE	-	-	-
	p	Intercept	-1.41	0.15	-	-
		DM2	0.68	0.59	-	-

*Not model averaged

APPENDIX B

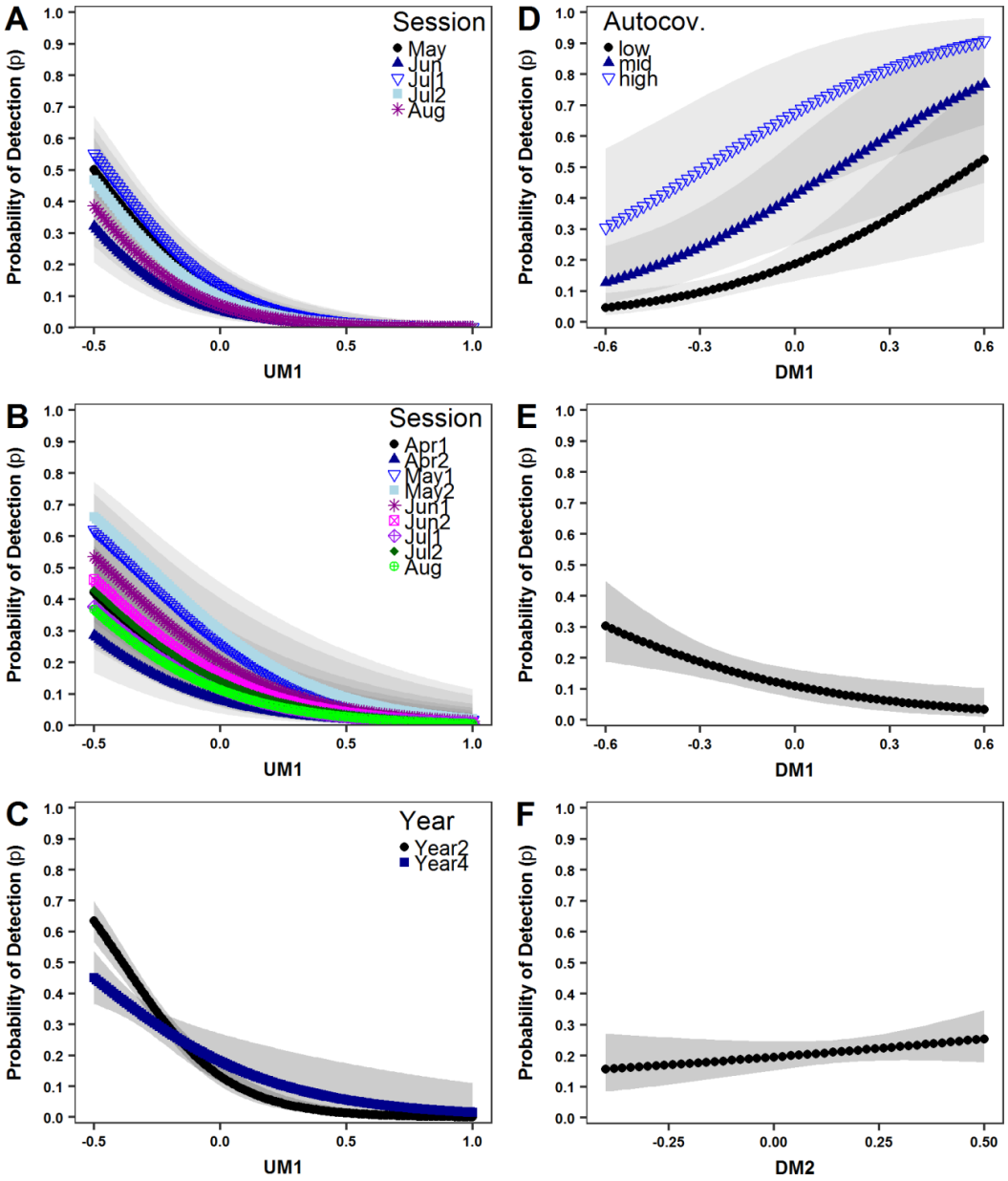

Figure B1 Model averaged probability of detection and 95% confidence intervals for *S. arenicolus* from the microhabitat models. (A-C) Undisturbed site, years 1, 3, and 2&4, respectively. (D-F) Disturbed site, years 2-4, respectively. Year 1 detection probability on the disturbed site was constant (p = 0.12 ± 0.03 SE). Abbreviations as follows: AUTOCOV = percent occupied surrounding sub-grids; DM1 = high average slope to high average compaction gradient; DM2 = high oak and litter cover to high sand cover gradient; UM1 = high average slope to high average compaction gradient; UM2 = high to low percent cover of oak and litter gradient.

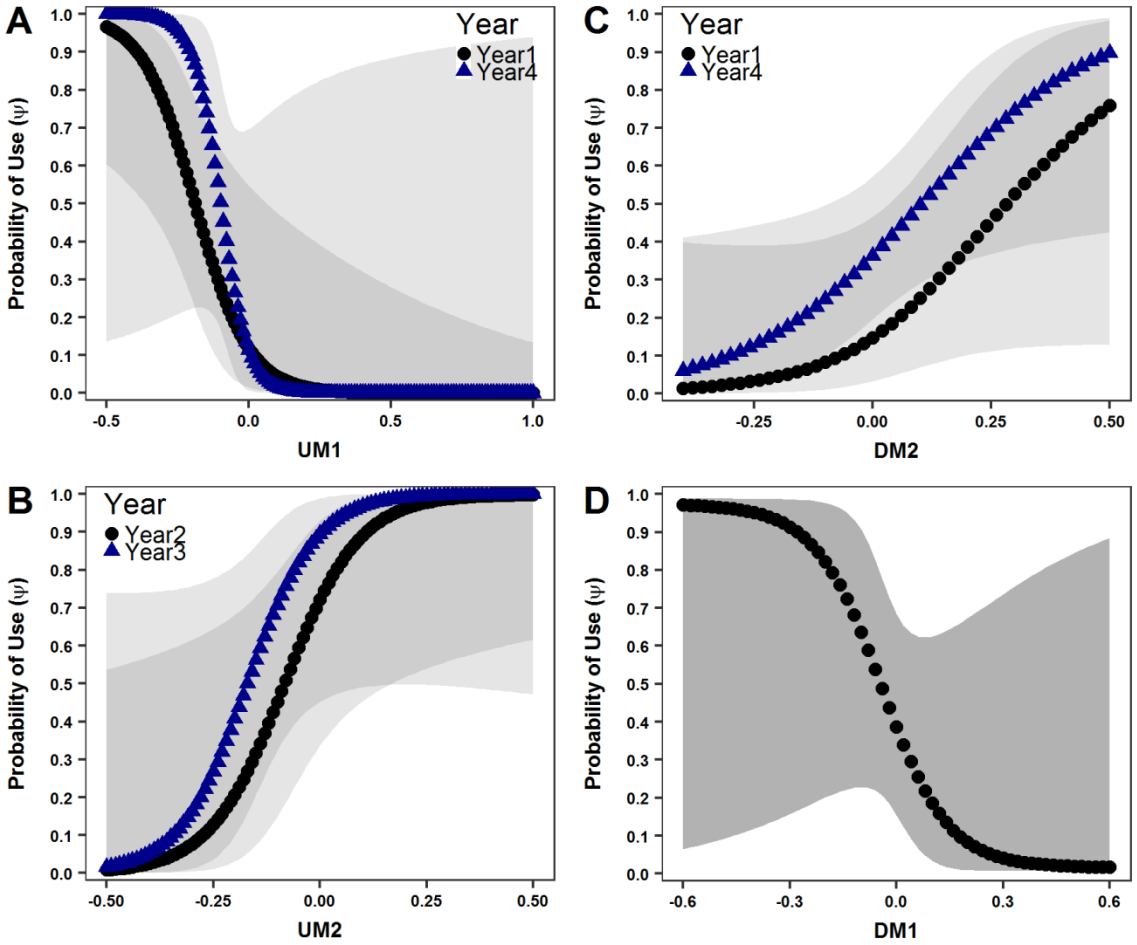

Figure B2 Model averaged probability of use and 95% confidence intervals for *S. arenicolus* from the microhabitat models. (A-B) Undisturbed site, years 1 & 4, and 2 & 3, respectively. (C-D) Disturbed site, years 1 & 4, and 2, respectively. Year 3 probability of use on the disturbed site was constant ($\psi = 0.07 \pm 0.06$). Abbreviations as follows: DM1 = high average slope to high average compaction gradient; DM2 = high oak and litter cover to high sand cover gradient; UM1 = high average slope to high average compaction gradient; UM2 = high to low percent cover of oak and litter gradient.

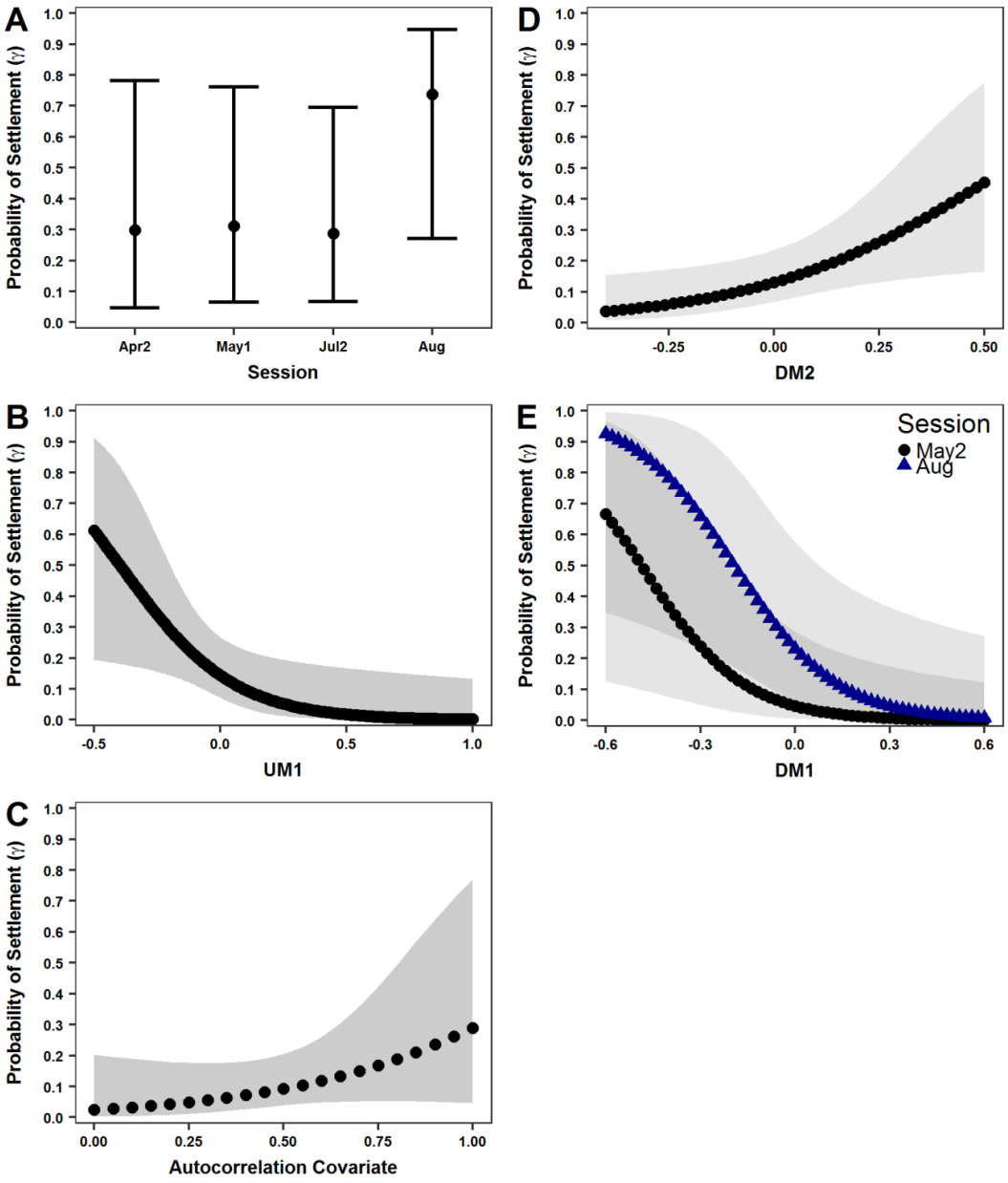

Figure B3 Model averaged probability of settlement and 95% confidence intervals for *S. arenicolus* from the microhabitat models. (A-C) Undisturbed site, years 2 - 4, respectively. (D-E) Disturbed site, years 3 - 4, respectively. Year 1 probability of settlement was constant (undisturbed $\gamma = 0.22 \pm 0.08$, disturbed $\gamma = 0.09 \pm 0.04$). Year 2 probability of settlement on the disturbed site was not estimable. Abbreviations as follows: AUTOCOV = percent occupied surrounding sub-grids; DM1 = high average slope to high average compaction gradient; DM2 = high oak and litter cover to high sand cover gradient; UM1 = high average slope to high average compaction gradient. Only the trap sessions where probability of settlement are estimable are shown for (A) and (E).

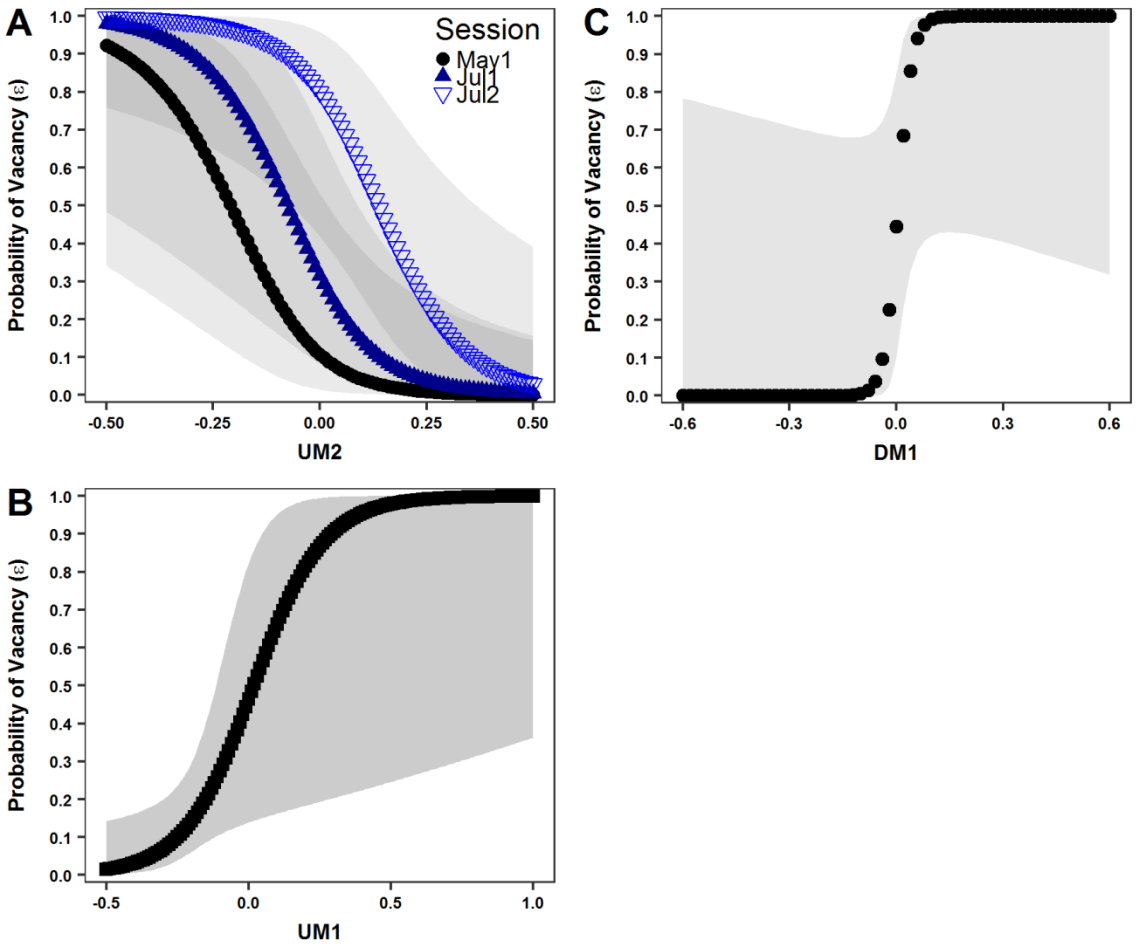

Figure B4 Model averaged probability of vacancy and 95% confidence intervals for *S. arenicolus* from the microhabitat models. (A-B) Undisturbed site, years 2 and 4, respectively. (C) Disturbed site, year 2. All other probabilities of vacancy for these models were not estimable. Only the trap sessions where probabilities of settlement are estimable are shown for (A).Abbreviations as follows: DM1 = high average slope to high average compaction gradient; UM1 = high average slope to high average compaction gradient; UM2 = high to low percent cover of oak and litter gradient.

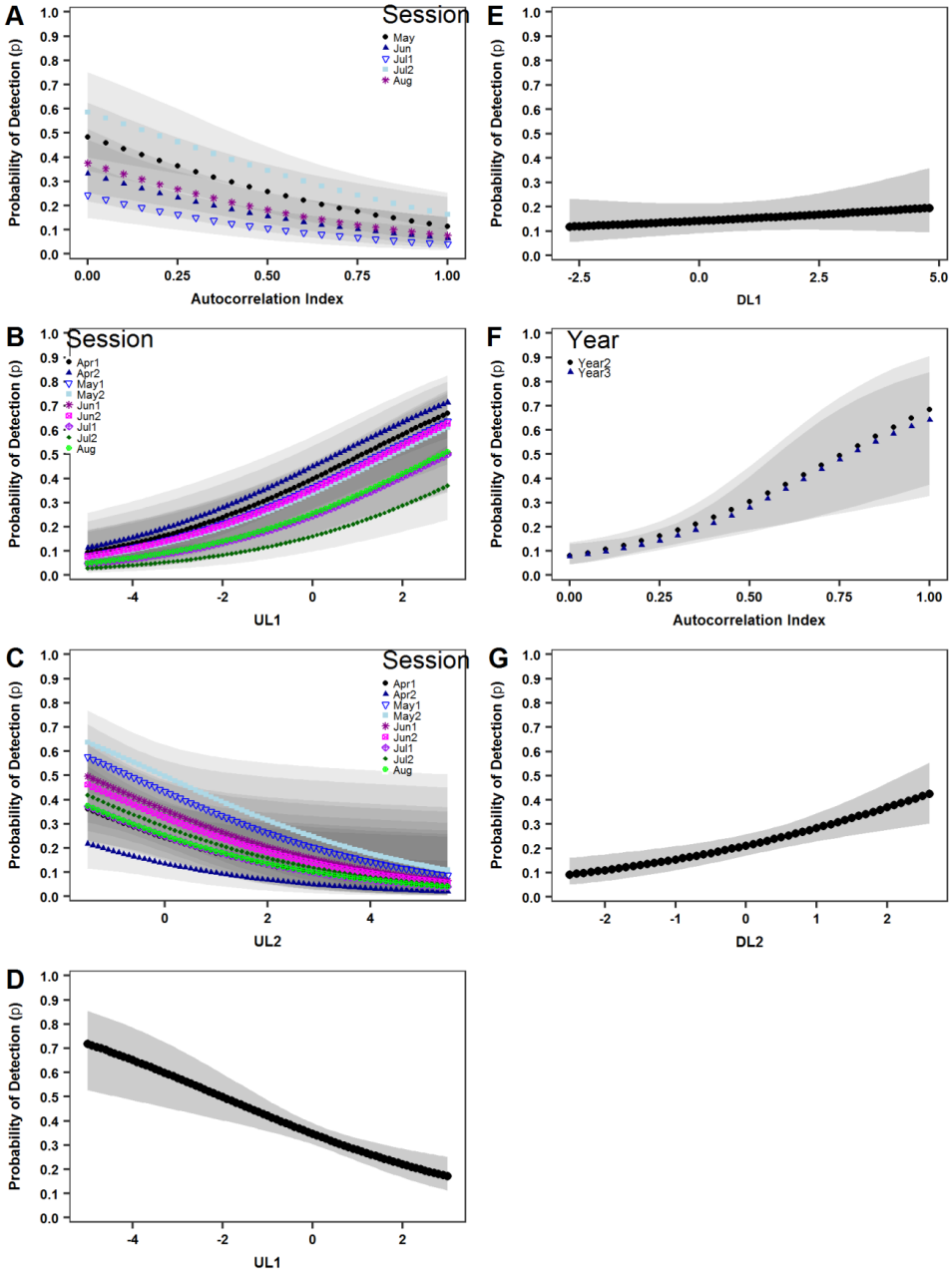

Figure B5 Model averaged probability of detection and 95% confidence intervals for *S. arenicolus* from the landscape models. (A-D) Undisturbed site, years 1-4, respectively. (D-F) Disturbed site, years 2-4, respectively. Year 1 detection probability on the disturbed site was constant (p = 0.12 ± 0.03 SE). Abbreviations as follows: AUTOCOV = percent occupied surrounding sub-grids; DL1 = large shinnery oak patches to large sand and road-well pad patches gradient; DL2 = highly aggregated sand patches to complex sand and shinnery oak patches gradient; UL1 = large, aggregated sand patches to small, disaggregated sand patches gradient; UL2 = large, complex shinnery oak patches to small, simple shinnery oak patches gradient.

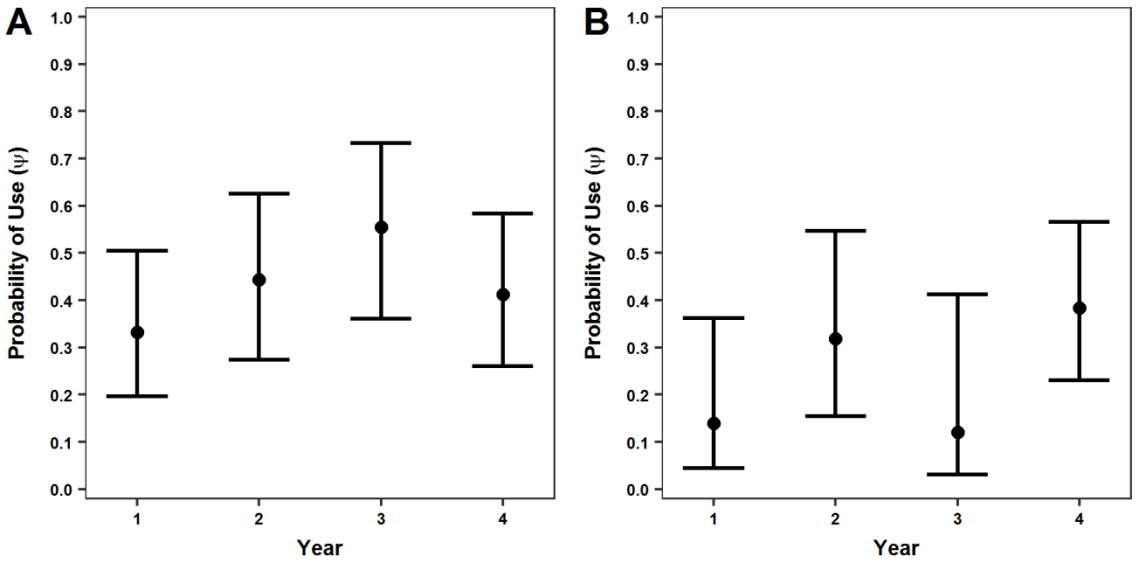

Figure B6 Model averaged probability of use and 95% confidence intervals for *S. arenicolus* from the landscape models. (A) Undisturbed site (B) Disturbed site.

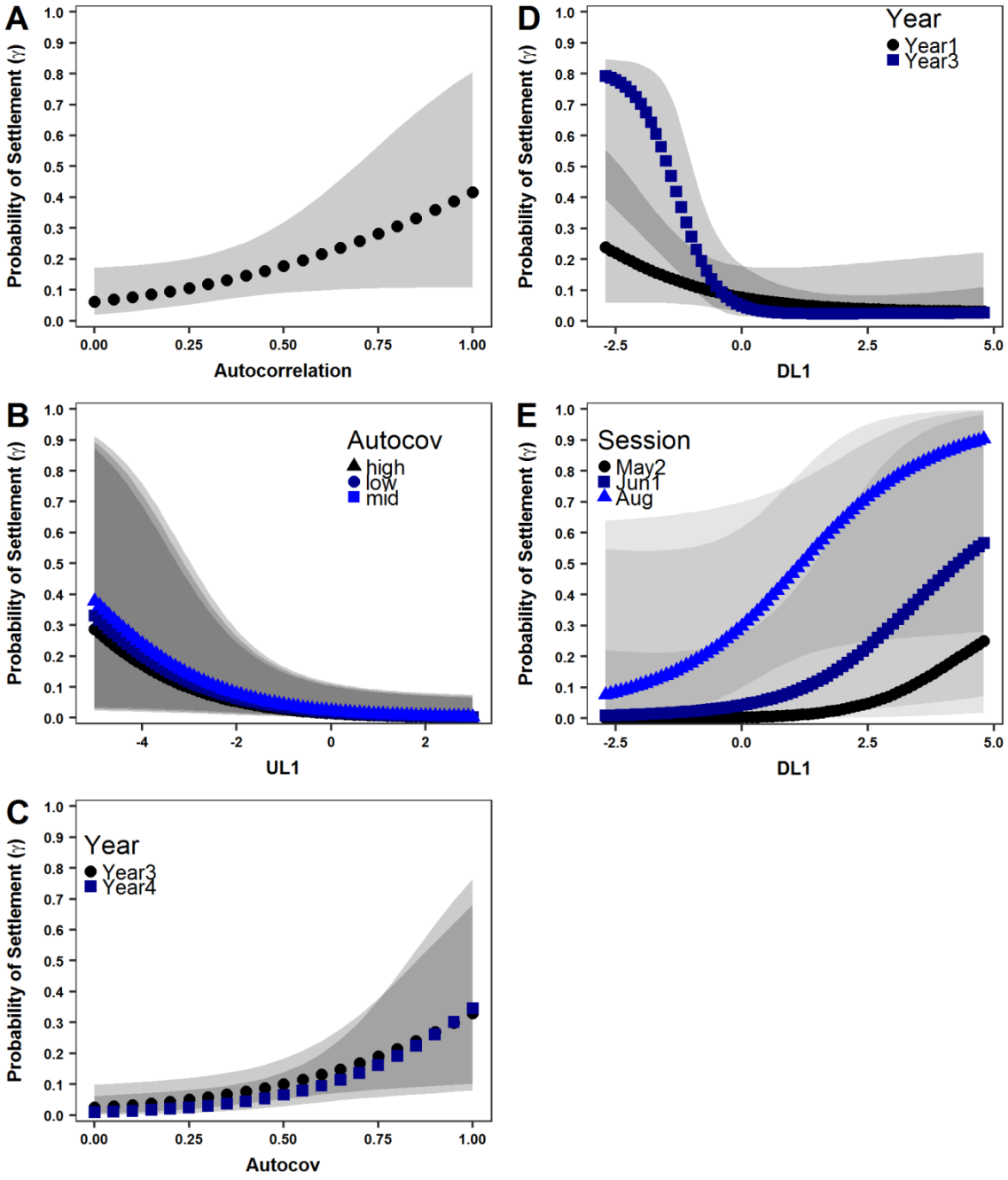

Figure B7 Model averaged probability of settlement and 95% confidence intervals for *S. arenicolus* from the landscape models. (A-C) Undisturbed site, years 1, 2, and 3&4, respectively. (D-E) Disturbed site, years 1&3, and 4, respectively. Year 2 probability of settlement on the disturbed site was 0.16 ± 0.07 SE. Abbreviations as follows: AUTOCOV = percent occupied surrounding sub-grids; DL1 = large shinnery oak patches to large sand and road- well pad patches gradient; UL1 = large, aggregated sand patches to small, disaggregated sand patches gradient.

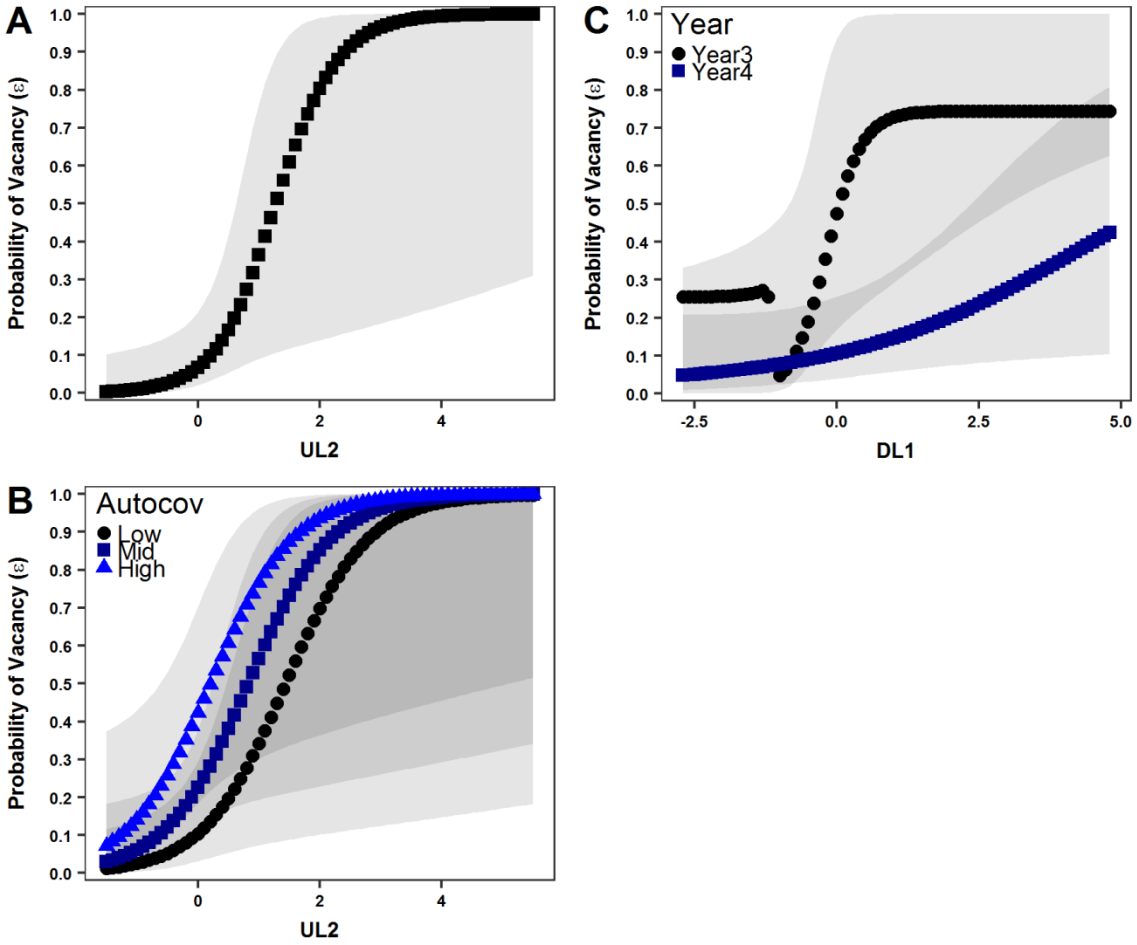

Figure B8 Model averaged probability of vacancy and 95% confidence intervals for *S. arenicolus* from the landscape models. (A-B) Undisturbed site, years 2 and 3, respectively. (C) Disturbed site, year 3&4. Probability of vacancy for year 1 on both sites was inestimable. Year 4 on the undisturbed site and year 2 on the disturbed site were constant (ε = 0.09 ± 0.03 SE and ε = 0.06 ± 0.02 SE, respectively). Abbreviations as follows: DL1 = large shinnery oak patches to large sand and road- well pad patches gradient; UL2 = large, complex shinnery oak patches to small, simple shinnery oak patches gradient.